Non-Harvest *Pinus radiata* Plantations for Forest Restoration in New Zealand

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A thesis

submitted in partial fulfilment

of the requirements for the Degree

of

Doctor of Philosophy in Forestry

by

Adam S. Forbes

New Zealand School of Forestry

College of Engineering

University of Canterbury

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1. ABSTRACT

New Zealand has lost *ca*. 71% of its former indigenous forest cover and this has contributed to the profound impacts and declining trends that have been reported for the state of New Zealand's indigenous biodiversity. Today *ca*. 7% of the land area is occupied by exotic plantation forest, 90% of which comprises *Pinus radiata* monocultures. Despite its exotic identity, these *Pinus* plantations are known to facilitate the regeneration of shade-tolerant indigenous forest flora. However, above-ground successional development is lost in commercial plantations when clear-fell forest harvest occurs. Over the life time of a plantation forest, for a range of social, economic, or environmental reasons management objectives might change meaning that plantation owners no longer intend to harvest their forest. Here I introduce the concept that "non-harvest" *P. radiata* plantations provide one option for the long-term restoration of indigenous forest cover in New Zealand.

This research addresses three research questions: (1) What are the long-term forest regeneration patterns in New Zealand's non-harvest *P. radiata* plantations? (2) Which ecological processes act to constrain indigenous forest regeneration processes? (3) How can management intervene to address these constraints, and thereby promote indigenous forest regeneration in exotic non-harvest *P. radiata* plantations?

To answer these questions, firstly, I surveyed a *ca*. ninety-year chronosequence of *P. radiata* plantations to examine patterns in plantation understorey regeneration and determine the main factors influencing forest regeneration. Secondly, I conducted an experimental canopy gap study within *ca*. 18-year-old *P. radiata* plantation forest to determine the potential for creation of small-scale artificial canopy gaps as a means of accelerating seedling growth rates of mature forest canopy species. Thirdly, I carried out experimental thinning of dense tree fern dominated *P. radiata* plantation understories to determine the potential of understorey thinning interventions as a means of accelerating seedling growth rates of mature forest canopy species. Fourthly, I surveyed a *ca*. 50-year-old podocarp underplanting trial to determine the potential for accelerating and directing forest succession by underplanting non-harvest *Pinus* stands with mature forest canopy species.

The findings of this research illustrate that the long-term structure and composition of *P. radiata* plantation understory regeneration is strongly influenced by both stand age and proximity to indigenous forest seed sources. The reliable natural establishment of large-

fruited, bird-dispersed mature forest canopy species requires the sheltered conditions provided by mature stands, proximal seed sources, and seed dispersal vectors. Creation of small-scale canopy gaps provides a means of increasing light transmission to the plantation understorey, and thereby optimising light levels for the growth of indigenous mature forest canopy species. Plantation understories comprising dense tree fern stands were found to significantly reduce both transmitted light and seedling growth rates of mature forest canopy species. Underplanting a degraded and ecologically isolated *Pinus* plantation with indigenous conifers accelerated successional development and provided a means of achieving dominance by mature forest canopy species within only 50 years.

This research shows that the sheltered conditions and long-term stability of "non-harvest" *P. radiata* plantations provide one means of restoring indigenous forest communities in New Zealand. This method of forest restoration is particularly relevant for lowland, commercially-productive, landscapes where indigenous forest loss has been greatest and where opportunities to restore indigenous forest are limited. The research also illustrates the important role of indigenous forest remnants as natural seed sources in the landscape, and thus the importance of maintaining indigenous remnants amongst commercially-productive landscapes. This research shows that while constraints on indigenous forest regeneration within *P. radiata* plantations do exist in the form of competition for light and limited indigenous seed dispersal, management interventions to address these limitations are possible and can successfully accelerate and direct indigenous forest regeneration in non-harvest *P. radiata* plantations. Thus, this research establishes that exotic "non-harvest" plantations can provide an important opportunity for the management and conservation of indigenous biodiversity in New Zealand.

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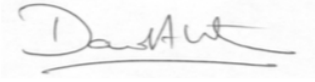
Name: *Professor David Norton* Signature:  Date: *9 October 2015*

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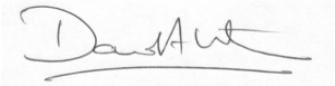
Name: *Professor David Norton* Signature:  Date: *9 October 2015*

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I carried out most of the planning of the survey, I undertook the survey, I undertook the data analysis, and I wrote the manuscript. I had assistance from my Superviors with designing the survey, and received guidance throughout the remainder of the research project, mostly through revisions of the manuscript and with advice regarding preparation of the manuscript for publication. Accordingly, I consider my contribution to Chapter Five has been approximately 90–95%. Adam Forbes.

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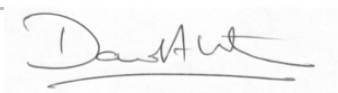
Name: *Professor David Norton* Signature:  Date: *9 October 2015*

2. CHAPTER ONE:

Introduction

2.1. WHY RESTORE INDIGENOUS FOREST USING EXOTIC PLANTATION FOREST?

2.1.1. Indigenous Forest Loss and Exotic Forest Gain

Up until *ca*. 1000 years ago, New Zealand was almost completely forested (Ewers et al., 2006; McGlone, 1983, 1989). However, since then, the extent of natural forest cover has been greatly reduced. An estimated 71% (14 million ha) of natural forest extent has been lost (Ewers et al., 2006), with patterns in forest loss having been skewed toward greater loss of lowland forests (Ewers et al., 2005), largely due to the attractiveness of alluvial flat lands for agriculture. As a consequence, of remaining natural forests, those in the lowlands are the most under-represented (Ewers et al., 2006, Norton, 2000, Norton & Miller, 2000), and where these forest remnants persist today they usually exist in a matrix amongst commercial production land uses (Norton, 2000), such as pastoral production or exotic plantation forests.

While natural forest cover has been reduced, New Zealand's contemporary lowland landscape features a range of forest types comprising exotic canopy species, some of which have the potential to nurse the regeneration of indigenous forest species (Williams, 2011; Sullivan et al., 2007). The most extensive exotic forest type is *Pinus radiata* which is normally established as a commercial timber crop (Ministry of Primary Industries [MPI], 2014). The extent of exotic plantation forests continues to expand, and as of 2014 planted forests occupied 7% of New Zealand's landmass (MPI, 2014). These forests are 90% comprised of exotic *P. radiata* (MPI, 2014). These exotic *P. radiata* plantation forests, despite their exotic identity, present opportunities for the regeneration of indigenous forest species (Brockerhoff et al., 2008a).

2.1.2. Use of Exotic Forests for Restoration

While the notion of restoring diverse indigenous forest communities using a planted exotic monoculture forest presents somewhat of a paradox (Lugo, 1997), the current

environments available for restoration are so highly modified that natural successions can take decades to centuries to establish and may even lack critical components required to achieve tall indigenous forest. Restoration of forest communities is particularly difficult in rain-shadow dryland zones (Rogers et al., 2005) or where highly competitive invasive plant assemblages have established, which then restrict the regeneration of future indigenous forest canopy species (Norton et al., 2009; Standish et al., 2001).

The existing literature shows that when fast growing species are used, the rapidly growing plantation trees quickly create sheltered conditions, moderating climatic variables, and in some cases will create an environment similar to that of natural forests (Parrotta et al., 1997). Creation of sites with moderated microclimatic conditions is likely to aid the restoration of indigenous forest species by reducing the barriers presented by climatic extremes which occur at open sites (Sullivan et al., 2009). The shade cast by the plantation canopy creates conditions less favourable to the highly-competitive light-demanding species which typically prevent regeneration at open sites (Parrotta et al., 1997). With time, the shade cast by the plantation canopy also has the potential to promote the establishment of shade-tolerant forest species (Brockerhoff et al., 2008a; Lamb et al., 2005).

In many tropical countries plantation forests have been used as a means of rehabilitating lands degraded by conversion from natural forest to agricultural land use (Lamb et al., 2005; Lamb, 1998; Parrotta et al., 1997). In these cases, rapid plantation forest growth provides a means of establishing shade-tolerant forest tree species sooner than those species would occur if reliant on the development of a natural nurse community to establish within, and this advantage has the effect of accelerating forest succession (Parrotta et al., 1997).

Examples of indigenous forest regeneration within plantation forests also come from outside of the tropics. In Southern Ethiopia, monoculture plantations of *Cupressus*, *Eucalyptus*, and *Pinus* were found to foster the regeneration of indigenous woody species (Senbeta et al., 2002), and Chilean *P. radiata* plantations were found to provide suitable conditions for the regeneration of dominant indigenous forest species (Guerrero & Bustamante, 2007). Indigenous forest regeneration has also been studied in New Zealand's commercial *P. radiata* plantation forests (Brockerhoff et al., 2003; Ogden et al., 1997; Allen et al., 1995; McQueen, 1973, 1961; Henry, 1954). We now know that commercial *P. radiata* plantations not only provide conditions suitable for the facilitation of shade-tolerant indigenous forest plants, but also increase landscape ecological connectivity (Norton, 1998), provide microclimate buffers to adjacent indigenous forest remnants (Denyer et al., 2006),

and, in some circumstances, these exotic forests even provide habitats for threatened species (Pawson et al., 2010).

2.1.3. The Opportunity of Non-Harvest *P. radiata* Plantations for Restoration

Currently, New Zealand's commercial timber plantations operate on a 25–30 year clear-fell harvest regime, and while there are clear benefits from managing these plantations to maximise biodiversity, this inevitably means that any above-ground successional development is truncated by plantation harvest and site reestablishment practices (Ogden et al., 1997). Although indigenous forest regeneration processes within exotic plantation forests have been widely studied, these studies have normally been set in the context of the ephemeral opportunities for forest regeneration in commercial plantations that are held under clear-fell harvest regimes. However, for a range of social, economic, or environmental reasons, management objectives might change over the life time of a plantation forest, meaning that plantation owners no longer intend to harvest their forest (Norton & Forbes, 2013; Cummings et al., 2007). Examples of motivations for plantation owners no longer wanting to harvest their exotic plantation forest include adoption of permanent carbon forest (MPI, 2015), or changes in the economic market meaning timber harvest is no longer desirable (Onaindia et al., 2013). Plantation forests might also be retired from the harvest regime for environmental reasons, such as where they are used water or soil conservation (Marden et al., 2012) and remain unharvested.

Given what we know about the potential role of plantation forests in facilitating (*sensu*: Connell & Slatyer, 1977) indigenous forest regeneration, these "non-harvest" plantations provide sites with forest microclimate conditions and long-term stability, and are therefore generally amenable to long-term forest regeneration. While research has been undertaken both in New Zealand and internationally into the role of exotic plantation forests in facilitating the regeneration of indigenous forest plants, the role of non-harvest exotic plantation forests in providing sites for the long-term restoration of indigenous forest has received much less attention, especially in a temperate environment such as occurs in New Zealand.

Motivated by the prospect of a declining economic market, the use of *P. radiata* plantations for restoration of indigenous mixed-*Quercus* forest, rather than timber production, was investigated in temperate Spain (Onaindia et al., 2013; Onaindia & Mitxelena, 2009). Exotic *P. radiata* plantations were found to promote the natural regeneration of indigenous forest species to an extent that *P. radiata* plantations were recommended as a long-term

means of restoring the mixed-*Quercus* forest (Onaindia & Mitxelena, 2009), although some differences were identified between mature *P. radiata* understorey compositions and old-growth natural mixed-*Quercus* forest (Onaindia et al., 2013).

However, the literature provides no comparable New Zealand examples of research into the management of non-harvest *P. radiata* plantations specifically for the long-term restoration of indigenous forest. Although the use of non-harvest *P. radiata* plantation forests is not the first choice of restoration methods for establishing indigenous forest cover in New Zealand, when the opportunity of non-harvest *P. radiata* plantations arise, I propose that these exotic planted forests present a potential means of restoring indigenous forest cover, particularly when plantations are managed with forest restoration objectives in mind. These sites conceivably provide important opportunities to restore indigenous forest cover in lowland areas where opportunities for the restoration of indigenous forest are often limited by either land use practices (MacLeod & Moller, 2006), or ecological barriers to forest regeneration (Zimmerman et al., 2000).

2.2. THESIS OBJECTIVES

This thesis seeks to address three primary objectives. The first objective is to examine the potential long-term role of non-harvest *P. radiata* plantations as a means of restoring indigenous forest cover in New Zealand. As patterns in *P. radiata* understory regeneration in New Zealand have rarely been studied in forests older than the extent of the commercial rotation length (25–30 years), I aim to provide an understanding of long-term forest regeneration patterns in New Zealand non-harvest *P. radiata* plantations (up to 90 years).

The second objective of this thesis is to understand the ecological processes that act to constrain indigenous forest regeneration patterns in New Zealand's exotic conifer non-harvest plantations. While acknowledging opportunities exist to use non-harvest *P. radiata* stands for indigenous forest restoration, I propose there are many potential barriers to forest regeneration processes that are associated with planted exotic *Pinus* stands, and which might require specific attention if *Pinus* stands are to be optimised for forest restoration outcomes. When non-harvest plantation forests are to be managed for the restoration of indigenous forest cover an understanding of these processes will assist forest managers and restoration practitioners in restoring indigenous forest species and transitioning exotic planted forests toward indigenous dominance.

After articulating the processes that constrain indigenous forest regeneration, the third objective of this thesis is to then describe interventions to address these constraints, and thereby promote indigenous forest regeneration in exotic non-harvest *P. radiata* plantations.

The following outline describes how I address these thesis objectives through this thesis.

2.3. THESIS OUTLINE

Through Chapter One I introduce New Zealand's current position regarding both indigenous forest loss and the expansion in cover of exotic conifer plantation forests. Here, I highlight that, for a range of reasons, management of some of these plantation forests might become "non-harvest", thereby presenting long-term opportunities for the restoration of indigenous forest cover. Having established this background, I then introduce the three thesis objectives which are: (1) to examine the potential long-term role of non-harvest *P. radiata* plantations as a means of restoring indigenous forest cover, and (2) to gain an understanding of the ecological processes that act to constrain indigenous forest regeneration patterns in New Zealand exotic conifer non-harvest plantations, and (3) to then describe interventions that can be used to optimise forest regeneration processes.

In Chapter Two I then focus on addressing the first thesis objective. To do this I will use a chronosequence of *P. radiata* plantation stands aged 2–89 years to assess understorey regeneration patterns. I propose that the establishment of indigenous species depends on both suitable light levels in the plantation understorey and also on the ability of species to reach the site via dispersal from nearby indigenous forest. From this chronosequence survey I illustrate patterns in long-term forest development in the understories of *P. radiata* plantations, and to gain insights into factors that might constrain these regeneration processes.

In Chapter Three I will investigate the competitive shading effect of the homogenous *P. radiata* plantation canopy on growth rates of two mature forest canopy species that have contrasting shade-tolerance and growth-rate related life history traits. I hypothesise that the creation of small-scale artificial canopy gaps within an 18-year-old *P. radiata* plantation would increase light transmission to the forest understorey, with the effect of accelerating seedling height growth rates. Using the results from this competition experiment I aim to investigate the degree to which the unmodified *Pinus* canopy constrains the growth of woody seedlings through shading, and how under these circumstances the creation of small-scale artificial canopy gaps of specific sizes can be used to accelerate seedling growth rates and

therefore assist forest restoration. Therefore, this chapter is relevant to, and will contribute towards, the second and third thesis objectives.

In Chapter Four I will build upon the existing knowledge regarding the competitive effects of tree fern dominance on forest regeneration processes, by investigating the competitive shading effect of tree fern dominated forest understories on the growth performance of two mature forest canopy species (*Pittosporum eugenioides* and *Podocarpus totara*) planted in New Zealand *P. radiata* plantation forest. I predict that the heavy shade cast by tree fern stands within mature *P. radiata* plantations will reduce the growth rate of these two canopy tree species. I will use indigenous forest species with differing shade-tolerance and growth-rate related life history traits, and examine their growth response to experimental manipulation of the tree fern canopy, which create heavy versus light shading of seedlings. This chapter is relevant to the second and third thesis objectives, in that it will provide insights into the effect of tree fern dominance on indigenous forest regeneration in New Zealand's *P. radiata* plantation forests, and will describe possible management interventions to help address tree fern competition when the promotion of indigenous forest regeneration is desired.

In Chapter Five I will examine the potential of underplanting as a restoration technique in non-harvest *Pinus* plantations. I do this by resurveying a *ca*. 50-year-old experimental trial where *ca*. 24 000 seedlings of three species of indigenous conifers were underplanted in a degraded *Pinus ponderosa* plantation. I hypothesise that the degraded *Pinus* canopy will provide suitably sheltered conditions for the development of a cohort of indigenous conifers, and that these indigenous trees would be structurally dominant on the site within 50 years of underplanting. This chapter will contribute to the second and third thesis objectives by assessing underplanting as a management intervention, and by then discussing the circumstances when underplanting might be particularly valuable for forest restoration within non-harvest *Pinus* plantations.

Chapter Six will then present a synthesis of the above research. I will discuss the long-term forest regeneration patterns within non-harvest *P. radiata* plantations, and the factors that I found to be controlling those regeneration patterns. In the context of the chronosequence survey results, I will discuss the potential of non-harvest *P. radiata* plantation forest for restoring indigenous forest cover (Thesis Objective One). I will then discuss the factors that I found to constrain indigenous forest regeneration within *P. radiata* plantations and give specific interventions that can be used to address these constraints, to

optimise *P. radiata* plantations for the restoration of indigenous forest cover (Thesis Objectives Two and Three).

As this thesis includes chapters that have been written for publication in scientific journals, I have structured the thesis in accordance with the University of Canterbury guidelines for including published material in a thesis. Chapter One provides a general introduction, and each subsequent data chapter has a "chapter preface", which describes the linkage among thesis chapters to aid continuity, and provides any details of the publication relating to the chapter. Chapter Six provides an overall conclusion. This style has produced some repetition amongst the content of thesis chapters. Tables and Figures are numbered from the beginning and therefore do not necessarily match the numbering of published manuscripts. All references are found at the end of the thesis to avoid repetition among chapters. Appendices are enclosed at the end of the thesis. The final appendix, Appendix K, is a published short paper that I was a co-author of in the early stages of my Ph.D. enrolment. It therefore represents part of my academic achievement during the course of my Ph.D. enrolment, and is enclosed for that reason, but is not a direct research output from my Ph.D.

3. CHAPTER TWO:

Indigenous Forest Regeneration in Exotic Non-Harvest *Pinus radiata* Plantations

CHAPTER PREFACE

Chapter Two aims to address the first main objective of this thesis, that is to examine the potential long-term role of non-harvest *P. radiata* plantations as a means of restoring indigenous forest cover. This chapter constitutes a chronosequence survey of forest regeneration patterns in central North Island *P. radiata* plantations, spanning a duration of nine-decades. In many respects the findings from Chapter Two provide a basis for subsequent data chapters (Chapters Three–Five), which focus on interventions to address some issues identified here. Where they exist, such linkages are explained in the corresponding chapter preface.

This thesis chapter has been written as a stand-alone scientific paper, with the intention of being submitted for publication in a scientific journal. At the time of thesis submission, the manuscript had not yet been submitted.

3.1. INTRODUCTION

Human habitation has caused vast reductions in the extent of natural forest cover across most of the world (Crowther et al., 2015), and an estimated 71% (14 million ha) of New Zealand's natural forest cover has been cleared (Ewers et al., 2006). This loss of forest habitat has diminished many aspects of forest-related biodiversity (Gardner et al., 2009; Brockerhoff et al., 2008a; Gaston et al., 2003) and a principal response has been the formulation of strategies to reduce further forest loss, to ensure that forests are managed sustainably, and that forest biodiversity is conserved (United Nations Environment Programme [UNEP], 1992). As of 2010, an estimated 6.6% (265 million ha) of the global forest area was planted forests, and New Zealand ranked ninth among the top-ten countries in absolute plantation area (Forest Stewardship Council [FSC], 2012). As increasing areas are afforested for timber production, methods to preserve or enhance indigenous biodiversity in these planted landscapes are also required (Carnus et al., 2006; Brockerhoff et al., 2001).

Existing research has examined the role of commercial plantations in facilitating the natural regeneration of indigenous forest flora (Brockerhoff et al., 2008a; Lamb et al., 2005). However, while commercial plantations might contribute ecologically by increasing landscape connectivity, buffering indigenous remnants, or providing sometimes scarce forest habitats (Brockerhoff et al., 2008a), the long-term potential for the recruitment of mature forest canopy species is usually truncated by the catastrophic disturbance associated with the plantation harvest and subsequent site preparation opperations (Chapman & Chapman, 1996; Allen et al., 1995). An estimated 90% of plantation forest in New Zealand comprises *Pinus radiata* (Pinaceae; Ministry of Primary Industries [MPI], 2014) and these commercial plantations operate on a clear-fell rotation of 25–30 years (MPI, 2014), meaning most of the indigenous regeneration is lost between harvest rotations. Alternatively, under some circumstances, for various environmental, social, or economic reasons, some *P. radiata* plantations are unlikely to be harvested, and these "non-harvest" stands present opportunities for the restoration of indigenous forest species, with associated benefits to indigenous biodiversity (Norton & Forbes, 2013).

Although the occurrence of indigenous forest regeneration in plantation forests has received more attention by researchers than has the long-term use of non-harvest plantations for forest restoration, several European surveys have assessed the role of *P. radiata* plantations as sites for the restoration of temperate forest species. On the Spanish Iberian Peninsula, under a changing economic market, the potential was assessed for *Pinus radiata*

plantations to be used as a passive restoration tool for the natural establishment of indigenous mixed-*Quercus* forest (Onaindia et al., 2013). It was found that with increasing plantation age, *P. radiata* plantations became compositionally more similar to natural *Quercus* forest, although diversity indices revealed *P. radiata* as maintaining a greater number of both rare and dominant species compared to *Quercus* stands, and several species indicative of old-growth forest were not found in the oldest *P. radiata* stands (aged 40 years; Onaindia et al., 2013). An earlier study emphasized the role of adjacent indigenous forest remnants in providing a source of propagules to enrich regeneration patterns in *P. radiata* plantations (Onaindia & Mitxelena, 2009).

Within *Pinus* plantations, two key predictors of understorey regeneration patterns are (1) stand age (Onaindia & Mitxelena, 2009; Keenan et al., 1997; Ogden et al., 1997) and (2) the proximity to indigenous forest seed sources (Zamora et al., 2010; Onaindia & Mitxelena, 2009; Zanne & Chapman, 2001). Age-related changes in the *Pinus* plantation canopy structure alter understorey illumination (Porté et al., 2004). These temporal changes in understorey light levels make stand age an important predictor of understorey regeneration patterns (Brockerhoff et al., 2003; Ogden et al., 1997), and indicators of forest development such as woody species richness have been found to be positively correlated with *Pinus* plantation age (Onaindia & Mitxelena, 2009; Keenan et al., 1997; Ogden et al., 1997). The proximity of indigenous forest seed sources to *Pinus* plantations is also of importance to patterns in understorey regeneration (Zamora et al., 2010; Onaindia & Mitxelena, 2009; Zanne & Chapman, 2001), which is particularly relevant to exotic *Pinus* plantations in New Zealand, where the flora is predominantly bird dispersed (*ca*. 70%; Clout & Hay, 1989), and most of this dispersal operates typically over short distances (Wotton & Kelly, 2012; Williams, 2006). It then follows that exotic conifer plantations, which do not produce nectar or fruit to attract key seed dispersing bird species, would have a limited ability to attract dispersers (Clout & Gaze, 1984), which imposes limitations on the ability of flora to establish within ecologically isolated *Pinus* plantations.

Little attention has been given to the potential of exotic non-harvest plantations as nurses for the long-term restoration of indigenous forest dominance in New Zealand. While the existing literature has been crucial for understanding regeneration patterns in commercial aged *P. radiata* plantations, questions remain over the long-term role of non-harvest *P. radiata* stands in providing opportunities for the restoration of New Zealand's indigenous forest communities.

Here we investigate the long-term potential of non-harvest *P. radiata* plantations in recruiting indigenous forest flora and developing a forest community dominated by indigenous woody species, characteristic of mature natural forest. We propose that the establishment of indigenous species is dependent on suitable light levels in the plantation understorey, and also on the ability of species to reach the site via dispersal from nearby indigenous forest. Corresponding to modifications of the understorey light environment from the rapidly closing *Pinus* canopy, we expect an initial invasion of light-demanding early-successional woody species, followed by an accrual of shade-tolerant indigenous angiosperm forest canopy species. We propose that mature *Pinus* stands provide suitable light levels for the establishment and growth of angiosperm canopy species, but that larger-seeded angiosperm species that are dependent on birds for dispersal will be limited in occurrence by their isolation from an indigenous forest seed source, regardless of *Pinus* stand age. We also expect that the relatively light-demanding conifer species of the Podocarpaceae family, which normally fill prominent canopy and emergent tiers in New Zealand's natural forests, would not be present in mature *Pinus* stands due to either dispersal limitation or the heavy shade cast by a combination of both the *Pinus* canopy and dense understorey vegetation. To represent natural forest regeneration over a period of nine decades following plantation establishment, we surveyed structural and compositional aspects over a chronosequence of *P. radiata* plantation stands aged 2–89 years, and compared these results with an old-growth indigenous forest reference site located within the study area.

3.2. METHODS

3.2.1. Study Area

The study was undertaken in Kinleith Forest, which is a large (*ca*. 66 000 ha) commercial exotic plantation forest located in New Zealand's central North Island (38°23'28"S 175°57'40"E). The climate is cool and moist. Average annual (1931–1990 average from Tokoroa in the middle of the study area; National Institute of Water and Atmospheric Research [NIWA], 2015) air temperature is 12°C, and monthly average temperatures range from 17°C (February) to 7°C (July). Average maximum and minimum air temperatures are 23°C (February) and 2°C (July), respectively. The annual average (1931–2003 average) rainfall is 1485 mm; average monthly rainfall ranges from 86 mm (March) to 156 mm (June).

Soils of the study area are Pumice and were formed from Tephra parent materials (Table 1; Landcare Research [LCR], 2015). These soils are characteristically coarse textured and free draining. Topography is variable and elevations range from 350 to 550 m above mean sea level (Table 1).

Mixed conifer-angiosperm forest is characteristic of the natural forests of the study area (Leathwick & Mitchell, 1992). These forests typically comprise the angiosperm mature forest canopy species: *Beilschmiedia tawa* (Lauraceae), *Hedycarya arborea* (Monimiaceae), *Knightia excelsa* (Proteaceae), and *Weinmannia racemosa* (Cunoniaceae); and Podocarpaceae conifers: *Dacrydium cupressinum*, *Podocarpus totara*, *Prumnopitys ferruginea*, and *Prumnopitys taxifolia*. However, the extent of these forests within the study area has been reduced to a point where only small forest remnants exist. Larger tracts of indigenous forest occur > 15 km to the south (Pureora Forest Park) and the north (Kaimai-Mamaku Forest Park) of the study area.

3.2.2. Chronosequence Design

For the purposes of a space-for-time substitution, we selected nine *P. radiata* plantation stands ranging in age from 2–89 years from establishment. The data describing stand age, silvicultural history, and underlying soils were provided by the Forest Manager, Hancock Forest Management. As the number of stands older than the commercial harvest rotation length (25–30 years) was limited, and considering that an even distribution of stand ages was required, the limited number of older stands suitable for inclusion in the chronosequence dictated the time-sequence spacing necessary for the < 30-year-old stands. Given that replication of plantation stands was not possible, we are unable to generalise some of our findings, such as those relating to the importance of indigenous forest proximity, and in these instances we signal any limitations and our conclusions are framed as hypotheses for further research (Davies & Gray, 2015). Stands were located within an approximately 35 km extent of the wider plantation forest. *Pinus radiata* stand selection aimed to vary only stand age and kept the following factors as uniform as possible: underlying soil type, topography, aspect, slope, consistency of silviculture interventions, stand size and shape sufficient to avoid edge effects, and proximity to other chronosequence stands. Chronosequence stand details are provided in Table 1.

3.2.3. Indigenous Forest Proximity

The Mean Proximity Index (*PX*; McGarigal & Marks, 1995) was used to provide a measure of proximity to indigenous forest for each plot surveyed within the *Pinus* chronosequence. The original *PX* is the sum of the ratio of indigenous forest patch size to distance from a focal patch to each indigenous forest patch (squared) within a search radius. However, we adapted the index to suit our plot based study. Rather than calculating the edge-to-edge distance between each indigenous patch and the focal *Pinus* stand, we calculated the distance from the indigenous forest edge to the *Pinus* plot center. Therefore, we expressed *PX* as the sum of indigenous forest patch area (m^2) within the search radius, divided by the sum of all indigenous edges to *Pinus* plot (squared (m^2)) distances, for all indigenous forest patches whose edges were within 1 km (linear) of the focal plot center. We chose 1 km lineal distance as the search radius due to its ecological relevance as a distance common New Zealand indigenous forest birds are unlikely to reliably disperse fleshy-fruited propagules (Wotton & McAlpine, 2015).

3.2.4. Field Survey

In each of the nine stands, and in the indigenous forest reference site, four 10 × 10 m understorey vegetation plots were randomly located and then surveyed. Plots were separated by a minimum of 50 m, and to avoid edge effects, plots were not located within 30 m of the plantation edge. Woody understorey plant cover, height, density and tree diameter (> 2 cm diameter at 1.35 m above ground level; dbh) were assessed within understorey plots using the RECCE method (Hurst & Allen, 2007). Cover-abundance for each understorey species was estimated using the scale: 1 = < 1%, 2 = 1-5%, 3 = 6-25%, 4 = 26-50%, 5 = 51-75%, and 6 = 76-100%. Understorey species were recorded when they had live foliage present within the height tiers: < 0.3, > 0.3-2, > 2-5, > 5-12, > 12-25, > 25 m. Woody epiphytes were tallied separately. Where woody epiphytes occurred on tree fern trunks, those epiphytes were identified to species level, the total number of woody epiphytes per tree fern was counted, and the host tree fern species identity was noted. To assess the degree of crowding by adjacent tree ferns, where a woody epiphyte was present, the structure of the surrounding tree fern stand was assessed using a basal area sweep (Factor 4; Bitterlich, 1984) centered on the host tree fern. Tree fern heights were measured to the lowest live frond. All saplings (< 2 cm diameter at breast height (dbh) & > 1.35 m tall) and seedlings (< 1.35 m tall) occurring within each 10 × 10 m understorey plot were identified to species level and tallied. Seedlings were tallied according to the height classes: < 15, 16-45, 46-75, 76-105, 106-135 cm. All *P. radiata*

trees occurring within a circular 0.03 ha plot centered on the understorey plot were identified and their dbh and height recorded. Tree heights were measured using a Vertex III hypsometer.

At each plot center, we assessed topographic exposure using the Meso-scale Topographic Index (McNab, 1993), which required measurement of eight equidistant slope to horizon measurements from each plot center. Also measured at each plot were aspect, slope, physiography, canopy structure, and light transmission. Canopy structure and light transmission were measured using hemispherical (fisheye) photographs, taken from plot centers at 1.35 m above ground level, using a Pentax K200 DSLR fitted with a Sigma 4.5 mm circular hemispherical lens. The proximity of *Pinus* stands to indigenous forest was mapped using a combination of aerial photography and field inspections to verify vegetation extent and composition. Plant nomenclature and dispersal mode follows the New Zealand Plant Conservation website (www.nzpcn.org.nz, accessed September 1, 2015).

Table 1. Forest stand details of the Kinleith Forest *Pinus radiata* plantation chronosequence, central North Island, New Zealand

Year Planted	Age	Silvicultural Treatment	Current Rotation	Soil Type^	Slope Aspect	Meso-scale Topography	Elevation	Coordinates
2013	2	P = 1; R = 1	3	TpH + NaH	3-18°, S	6.3	350	38°24’25”S 175°54’33”E
2009	5	P = 1; R = 1	3	TpH + NaH	0-22°, E	12.0	350	38°23’53”S 175°55’45”E
1999	15	T = 7	2	TpH + NaH	22-28°, E	11.4	450	38°22’38”S 175°56’15”E
1989	25	T = 6, 8	2	TpH + NaH	13-33°, N	9.8	350	38°24’06”S 175°55’14”E
1979	35	T = 7	2	OiH	17-30°, N	19.2	450	38°22’48”S 176°00’40”E
1970	44	–	1	W	25-35°, N	17.4	350	38°06’47”S 175°56’09”E
1954	60	T = 23	2	TpH	4-25°, S	12.8	350	38°23’57”S 175°58’22”E
1927	86	T = 16	1	TpH	0-25°, E	9.1	450	38°24’53”S 176°03’12”E
1925	89	–	1	Tpd	0-6°, E	4.1	350	38°16’40”S 175°50’18”E
N/A	NF	N/A	N/A	Na + Oi	5-24°, S	6.5	550	38°27’43”S 176°02’58”E

Note. Silvicultural treatments are: “P” = herbicide land preparation, “R” = herbicide release spray, “T” = thinning,”–“ = no data available; the numeral(s) indicate the plantation age (yrs.) at the time of silvicultural treatment(s). Elevations given are in 100 m vertical bands. Aspects given are the stand mean represented as the nearest cardinal direction. ^Soil abbreviations are: TpH = Taupo hill soils, Tpd = Taupo deep sand, NaH = Ngakuru hill soils, Na = Ngakuru loam, Oi = Oranui sand, OiH = Oranui hill soils, W = Waiohotu (silty loam). “NF” = natural forest reference site. Coordinates are shown in the WGS84 coordinate system.

Table 2. Chronosequence stand summary statistics. Kinleith Forest *Pinus radiata* plantation chronosequence, central North Island, New Zealand. Forest stand statistics refer to *Pinus radiata* only

Year Planted	Age (Years)	*n*	Density (Stems ha^{-1})	Basal Area (m^2 ha^{-1})	Mean Diameter (cm)	Canopy Height (m)	PX
2013	2	62	542±86	0.13±0.03	2.2 ±0.05	1.7 ±0.02	0.117
2009	5	67	558±34	8.7±0.6	14±0.4	9.2±0.2	0.001
1999	15	48	400±45	46±3	37±1	26±1	0.000
1989	25	24	200±36	43±5	52±2	38±1	0.041
1979	35	37	308±28	65±8	50±2	36±2	0.867
1970	44	39	325±34	55±3	45±2	31±1	54.774
1954	60	29	167±24	71±11	70±5	46±3	0.006
1927	86	15	125±25	82±23	89±6	55±3	0.066
1925	89	17	142± 44	107±30	95±6	52±2	0.000

Note. *n* = number of trees sampled. *PX* = Proximity Index: A landscape scale index representing the degree of ecological isolation of survey plots within *Pinus* stands from adjacent indigenous forest cover.

3.2.5. Statistical Analysis

All statistical analyses were undertaken using R (R Development Core Team Team [R], 2015). The effect of *Pinus* stand age on *Pinus* basal area and indigenous tree fern basal area were assessed using Generalised Linear Regression, applying the Gaussian family, and logarithm (for *Pinus*) and identity (for tree ferns) links, with natural log conversion of the explanatory variable: *Pinus* stand age. All regression models were tested for linearity, normality of the residuals, and homoscedasticity using diagnostic plots.

The relationships between both percentage canopy openness and percentage Photosynthetically Active Radiation (PAR), and *Pinus* stand age, were estimated using nonparametric Generalised Additive Models (GAM), through use of the mgcv package (Wood, 2011). These GAMs were applied using betar family and logit link function.

Woody epiphyte abundance was modeled as a function of tree fern host species identity, host tree fern trunk height, and surrounding tree fern stand density using a GLM, and applying Quasipoisson family and log link, with natural log conversion of the explanatory variable: tree fern stand density. For assessment of epiphyte abundance, tree fern stand density was determined for tree fern hosting woody epiphytes by multiplying the prism-derived stem count by four (the prism factor). Mean indigenous woody species richness (*S*; alpha diversity) was modeled as a function of stand age and meso-scale topographic exposure using a GLM, applying Quasipoisson family, and log link function, with an offset term being called for number of plots per stand. For GLMs, model selection constituted retaining significant predictors.

Differences among *Pinus* stands of varying age, and between *Pinus* stands and the indigenous reference site, for the following variables were assessed using nonparametric Kruskal-Wallis rank sum tests. Kruskal tests were applied in this regard to: percentage canopy openness, percentage PAR transmission, woody indigenous seedling densities, sapling densities, and indigenous tree basal area. Where Kruskal tests returned statistically significant results at alpha = 0.05, pairwise post-hoc tests were carried out using Nemenyi tests. The significance of differences in mean *Pinus* basal area between 86- and 89-year-old stands was tested using a Wilcoxon rank-sum test. Any association between indigenous tree basal area within *Pinus* stands and *Pinus* stand age was assessed using the nonparametric Spearman's rank-order correlation.

Species turnover (beta diversity) was assessed from woody species presence-absence data using Jaccard similarity that was calculated using the Simba package (Jurasinski & Retzer, 2012). The comparison of Jaccard similarity between paired stand ages provided an assessment of changes in the level of continuity in species composition over time. The possible spatial distribution of species across a pair of quadrats is expressed as follows: *a′* representing the total number of species common between both plots, *b′* representing the total number of species that occur in the neighbouring plot but are absent from the focal plot, and *c′* representing the total number of species that occur in the focal plot but not in the neighbouring one. Species turnover as expressed by *a′*, *b′*, and *c′* was visualized in similarity space using a Ternary plot in accordance with the approach advocated by Koleff et al. (2003).

Nonmetric dimensional scaling (nMDS) was used to make inferences regarding compositional shifts, both across the *Pinus* chronosequence and in relation to the indigenous forest reference site, using the metaMDS function of the Vegan package (Oksanen et al., 2008). For nMDS ordination analysis, species importance values were calculated following Allen et al. (1995). The following weights were allocated to the RECCE cover classes (cover class = weight): 1 = 1.0, 2 = 2.0, 3 = 3.0, 4 = 4.0, 5 = 5.0, and 6 = 6.0. Epiphytes were given a nominal weighting of 0.5. Differences in ordination space among the different aged *Pinus* stands and the indigenous forest reference site were tested using Permutational Multivariate Analysis of Variance with the adnois function in Vegan. The contribution of within-site variability was assessed using the function betadisper in Vegan. The nMDS ordination was further examined through similarity percentage analysis (SIMPER; Clarke, 1993) to distinguish which species discriminate between stand ages and between the two forest types.

Canopy structure and light transmission data were extracted from hemispherical photographs using the imaging software Gap Light Analyzer (GLA, Version 2; Frazer et al., 1999). For GLA modeling, the growing season was defined as 1 September–31 March, the default solar constant used was 1367 Wm^{-2}, and the default Cloudiness Index, Spectral Fraction, and Beam Fraction were all set at 0.5.

3.3. RESULTS

3.3.1. *Pinus radiata* Basal Area and Canopy Height

Stand age was a significant predictor of *P. radiata* basal area across the chronosequence ($F_{1,7} = 74.466$, $P < 0.001$; Fig. 1). Predicted *P. radiata* basal area increased from

9.7±4 m^2 ha^{-1} at year 2, to 49.6±5 m^2 ha^{-1} at year 30, and to 95.3±7 m^2 ha^{-1} at year 90. *Pinus* canopy height increased rapidly during the initial 25 years, and more gradually thereafter, reaching an eventual mean canopy top height of 53.8±1.6 m (n = 32) in 86- and 89-year-old stands. Chronosequence stand summary statistics are given in Table 2.

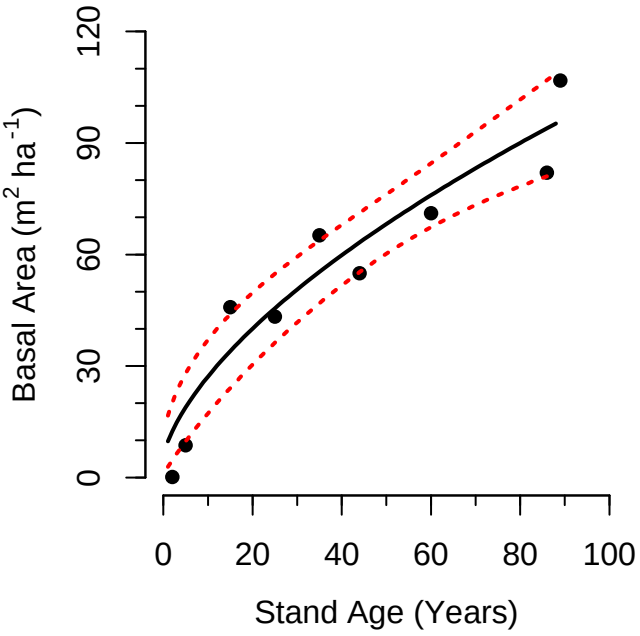


Figure 1. Generalised Linear Regression of *Pinus radiata* basal area from nine *P. radiata* plantation stands aged 2–89 years, located in Kinleith Forest, central North Island, New Zealand. Dashed lines indicate the 95% CI.

3.3.2. Canopy Openness and Total PAR Transmission

Predicted mean percentage canopy openness decreased from initially completely open canopy, to 33±4% 15 years after establishment, and to 12±3% at 20 years, beyond which canopy openness plateaued at about 8% for the remainder of the chronosequence. Percentage canopy openness differed significantly across the chronosequence ($X^2(9) = 34.013$, $P < 0.001$). The 2- and 5-year-old stands had significantly greater canopy openness compared to the older stands of the chronosequence. The amount of total PAR transmitted to the forest understorey differed significantly across the chronosequence ($X^2(9) = 32.103$, $P < 0.001$). Over the first 15 years, total PAR transmission was reduced from about 100% to 30±6% (Fig. 2). The degree of light transmission to the forest understorey plateaued 25 years after plantation establishment; beyond 25 years, only about 25% of total available light reached the forest understorey. No significant differences in either canopy openness (all $P > 0.14$) or total PAR transmission (all $P > 0.23$) occurred among stands aged 15 years or older. Nor were there significant differences in either canopy openness (all $P > 0.22$) or total PAR transmission (all $P > 0.14$) between stands aged 15 years or older and the indigenous forest reference site.

3.3.3. Forest Understorey Vegetation Structure

Woody seedling density

Indigenous woody seedling densities differed significantly among *P. radiata* stands of differing ages, and also differed from the seedling densities in the indigenous reference site ($X^2(9) = 27.348$, $P = 0.002$; Fig. 3). The highest indigenous woody seedling density within *Pinus* stands was found in the 44-year-old stand (3050±581 stems ha^{-1}; $n = 122$), where a significantly greater stem density was achieved compared to either 2- (25±25 stems ha^{-1}; $P = 0.021$) or 86-year-old *Pinus* stands (50±50 stems ha^{-1}; $P = 0.025$). Indigenous woody seedling densities in all stands other than those aged 2 and 86 years were not significantly different to the seedling density in the indigenous forest reference site (3750±1475 stems ha^{-1}; $n = 148$; all $P > 0.35$). Exotic seedlings were found in low densities in the 5-year (50±29 stems ha^{-1}; $n = 2$), 15-year (75±49 stems ha^{-1}; $n = 3$), and 25-year-old (125±95 stems ha^{-1}; $n = 5$) stands, and were absent from all other stands of the survey.

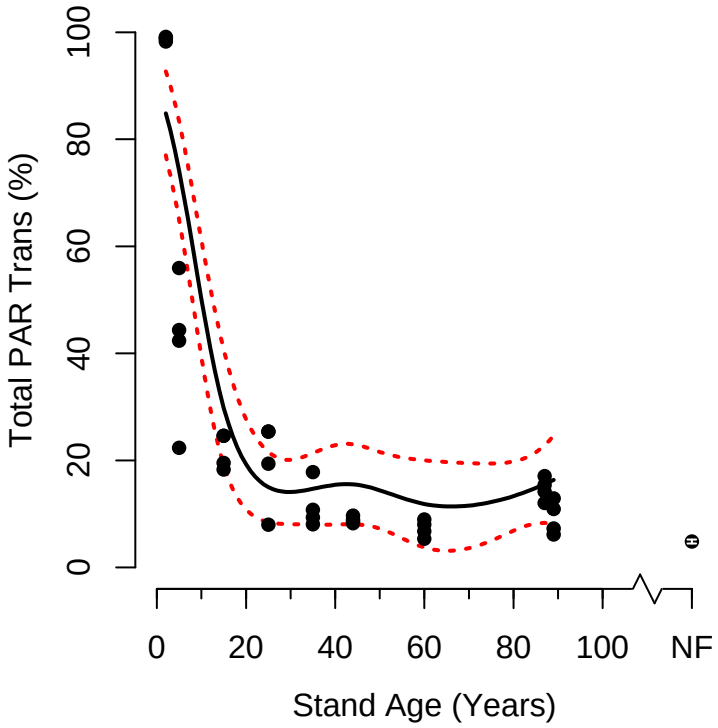


Figure 2. Fitted Generalised Additive Model of the percentage total photosynthetically active radiation (PAR) transmission assessed using hemispherical photographs taken at 1.35 m above ground level in a chronosequence of nine *Pinus radiata* plantation stands age. Dashed lines indicate the 95% CI. Mean value (±1SE) from the old-growth natural forest ("NF") reference site shown for comparative purposes.

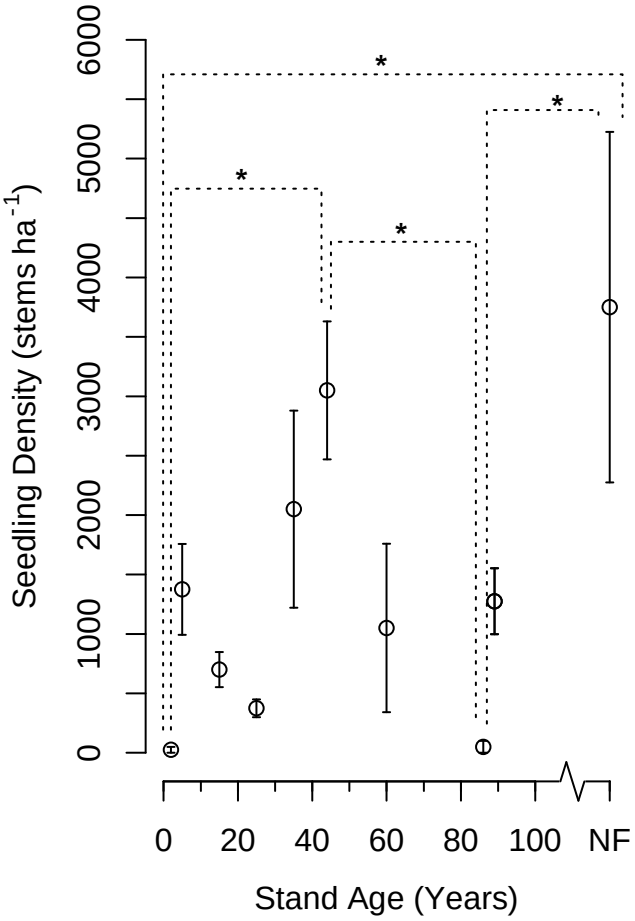


Figure 3. Indigenous woody seedling densities across a chronosequence of nine *Pinus radiata* plantation stands aged 2–89 years, Kinleith Forest, central North Island, New Zealand. The notation * indicates significant differences in mean values at the significance level $P < 0.05$. Error bars = ±1SE. Mean seedling density from an old-growth natural forest ("NF") reference site shown for comparative purposes.

Sapling density

The density of indigenous saplings differed significantly across the chronosequence ($X^2(9) = 26.58$, $P = 0.002$). The contributing differences were between the 2-year-old stand (where saplings were absent) and both the 35-year-old stand (1525±394 stems ha^{-1}; $P = 0.05$; $n = 61$) and the indigenous forest reference site (2525±812 stems ha^{-1}; $P = 0.023$; $n = 101$; data not shown). Exotic saplings were present in only the 5-, 15-, and 25-year-old stands; and were most numerous in the 5-year-old stand (625±239 stems ha^{-1}; $n = 25$) compared to either the 15-year (175 stems ha^{-1}; $n = 7$) or 25-year stands ($n = 1$).

Indigenous trees and tree ferns

There was no significant difference in indigenous tree basal area among the stands ($X^2(7) = 13.17$, $P = 0.068$), nor was there a significant association between indigenous tree basal area and stand age ($r_s(6) = 0.619$, $P = 0.115$; Fig. 4A). Adult tree ferns entered the chronosequence between years 15 and 25. Stand age was not a significant predictor of tree fern basal area across the chronosequence ($F1,4 = 6.170$, $P = 0.068$, Fig. 4B). Over the chronosequence, the tree fern community was dominated by *Dicksonia squarrosa* (Dicksoniaceae; range = 400±70–1125±433 stems ha^{-1}), with fewer numbers of *Cyathea medullaris* (Cyatheaceae; range = 0–475±95 stems ha^{-1}) and of *Cyathea dealbata* (Cyatheaceae; 0-125±75 stems ha^{-1}), and only a small number of *Dicksonia fibrosa* (Dicksoniaceae; $n = 2$). In the older (i.e., 44–89 years) *P. radiata* stands, mean tree fern heights were *D. squarrosa* = 3.8±0.2 m ($n = 119$), *C. medullaris* = 6.1±0.5 m ($n = 40$), and *C. dealbata* = 3.4±0.8 m ($n = 8$).

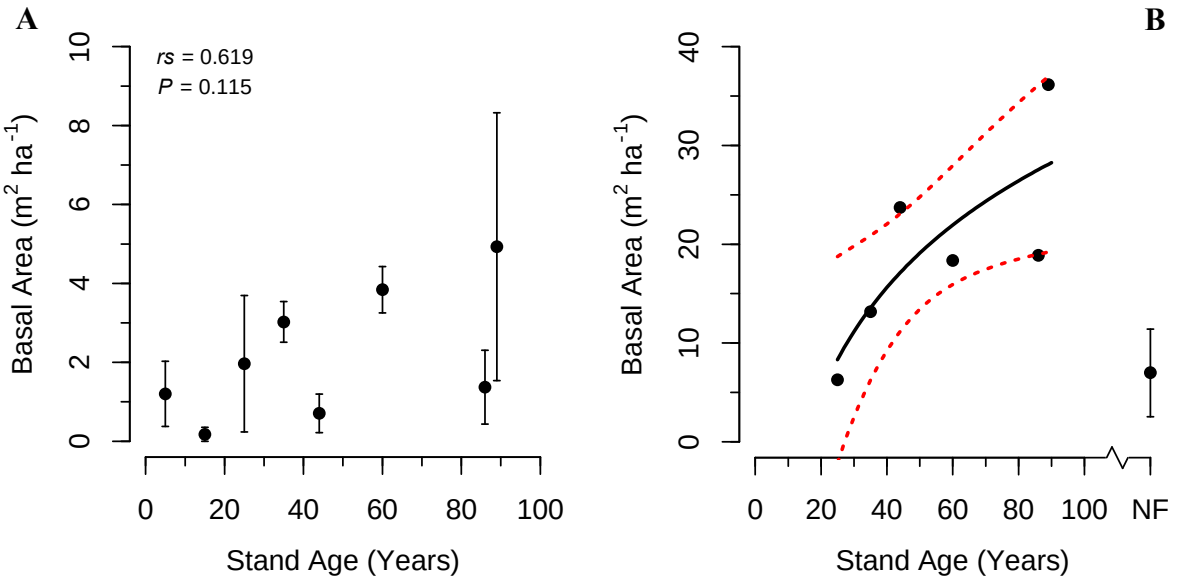


Figure 4. Basal area of indigenous (A) trees and (B) tree ferns across a chronosequence of nine *Pinus radiata* plantation stands aged 2–89 years, Kinleith Forest, central North Island, New Zealand. For comparative purposes, indigenous tree basal area at the old-growth natural forest was 164±33 m^2 ha^{-1} (not shown in Fig. 4A) and the tree fern basal area from the old-growth natural forest ("NF") is shown in Fig. 4B. Error bars = ±1SE; dashed lines indicate the 95% CI.

Indigenous woody epiphytes on tree ferns

Epiphytic establishment of indigenous woody species on tree fern trunks occurred in *Pinus* stands aged from 44 years and older, and was most common in the 86- and 89-year-old stands. The indigenous woody species found growing epiphytically on tree ferns were *Brachyglottis repanda* (Asteraceae; $n = 52$), *Pseudopanax arboreus* (Araliaceae; $n = 31$), *Geniostoma ligustrifolium* (Loganiaceae; $n = 24$), and *Melicytus ramiflorus* (Violaceae; $n = 4$). The greatest number of epiphytic woody seedlings counted on one tree fern was 19. The 86- and 89-year-old stands had comparable *Pinus* basal areas ($W = 9$, $P = 0.89$), and in these plantations, the tree fern basal area was the strongest predictor of woody epiphyte abundance ($P < 0.001$; Table 3). Epiphyte abundance was negatively associated with tree fern stand basal area (Fig. 5). Per linear meter of tree fern trunk height, *D. squarrosa* supported the greatest number of woody epiphytes (0.79 seedlings m^{-1}), compared to either *C. medullaris* (0.47 seedlings m^{-1}) or *C. dealbata* (0.22 seedlings m^{-1}).

Table 3. Analysis of Deviance Table from a Generalised Linear Model fitted to estimate the effect of tree fern trunk height, species, and surrounding tree fern basal area on the abundance of woody epiphytic plants growing on tree fern trunks. Data collected from host tree ferns surveyed in 86- and 89-year-old exotic *Pinus radiata* plantations, Kinleith Forest, central North Island, New Zealand

Analysis of Deviance Table: Woody Epiphytic Seedling Abundance				
	SS	Df	*F*	*P*
Tree fern height	6.487	1	3.408	0.082 †
Tree fern (host) species	12.804	2	3.364	0.059 †
Tree fern stand basal area	40.549	1	21.304	< 0.001 ***

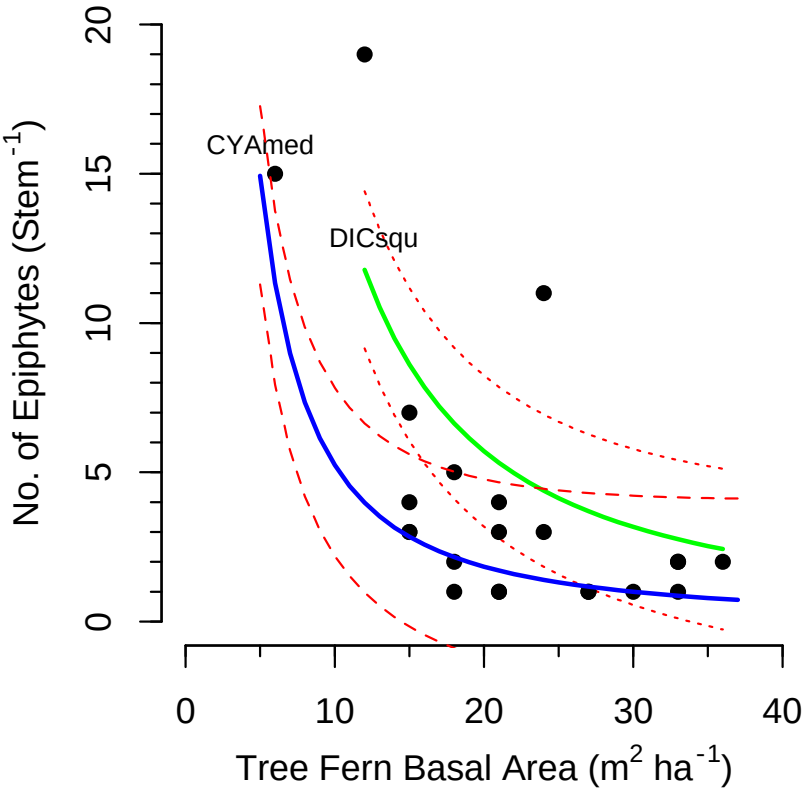


Figure 5. Predicted mean woody epiphyte abundance as a function of tree fern host species identity and surrounding tree fern stand density, holding tree fern height at mean value. Epiphyte data from two mature *Pinus radiata* plantations (aged 86- and 89-years-old) located in Kinleith Forest, central North Island, New Zealand. Species codes are: CYAmed = *Cyathea medullaris*, DICsqu = *Dicksonia squarrosa*. Although *Cyathea dealbata* (CYAdea) is included in the model, mean woody epiphyte abundance for CYAdea is not plotted to enhance clarity. Dashed lines indicate the respective 95% CI.

3.3.4. Species Richness

Stand age was a significant predictor of indigenous woody species richness (*S*) in plantations across the chronosequence ($F_{1,6} = 9.745$, $P = 0.021$; Table 4). Meso-scale topography was not a significant predictor of *S*. Early in the chronosequence, predicted *S* increased rapidly (2-year-old = 3.0±0.9 *S*, 10-year-old = 4.8±0.7 *S*, 20-year-old = 5.8±0.6 *S*) and more gradually thereafter (40-year-old = 7.1±0.7 *S*, 60-year-old = 8.0±0.9 *S*, 90-year-old = 9.0±1.2 *S*; Fig. 6). Although proximity to indigenous forest was not a significant predictor of *S,* the 44-year-old stand had the highest *S* of all plantation ages, and we found other evidence (seedling density, species turnover, and compositional data) to suggest a positive relationship between *S* and the close proximity to indigenous forest seed source. Therefore, the relatively high *S* sampled from the 44-year-old stand is likely to be resultant of factors other than stand age, such as proximity to seed source, aspect, or soil type. Exotic woody species richness was only a minor feature of the chronosequence, being limited to only 5-year-old (*S* = 1.5±0.3), 15-year-old (*S* = 1.25±0.3), 25-year-old (*S* = 0.5±0.3), and 44-year-old (*S* = 0.5±0.3) stands.

Table 4. Analysis of Deviance table from a Generalised Linear Model fitted to estimate the effect of *Pinus radiata* plantation age and meso-scale topographic exposure on the number of indigenous trees and shrubs found in the *P. radiata* understories. Data collected from a chronosequence of nine plantation stands ranging in age 2–89 years. Plantation stands located in Kinleith Forest, central North Island, New Zealand.

Analysis of Deviance Table: Woody Indigenous Species Richness

	SS	Df	*F*	*P*
Log Age	20.610	1	9.745	0.021 *
Meso-scale Topography	8.124	1	3.841	0.097 †

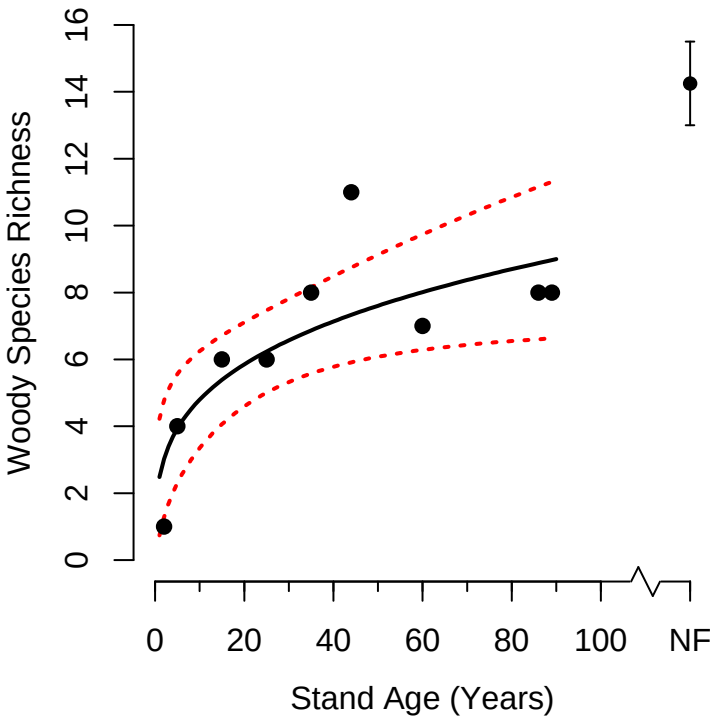


Figure 6. Predicted indigenous woody species richness (*S*) as a function of stand age and meso-scale topographic exposure, across a chronosequence of nine *Pinus radiata* plantation stands aged 2–89 years, Kinleith Forest, central North Island, New Zealand. For comparative purposes, the *S* from an old-growth natural forest ("NF") reference site is shown. Error bars = ±1SE; dashed lines indicate the 95% CI.

3.3.5. Species Turnover and Composition

Patterns in species turnover were related to stand age and proximity to indigenous forest. The 2-year-old stands were species poor, and shared few species with the more mature stands. These youngest stands featured light-demanding colonisers and were grouped in similarity space near the highest extent of axis *b´* and the lowest extent of axis *a´* (Fig. 7), signalling a high degree of species gain and low continuity in this young phase of the chronosequence. Five- and 15-year-old stands still showed < 50% similarity with stands of greater age. With only a few exceptions, stands > 25-years of age showed the greatest between-stand continuity, sharing similarity values of 50% or greater. The 44-year-old stand was a notable exception. It showed only about 30% similarity with stands of greater age, and about 55% of species were discontinuous between the 44-year-old stand and either of the three older stands. This result was driven by the high rate of occurrence of indigenous forest species in the 44-year-old stand.

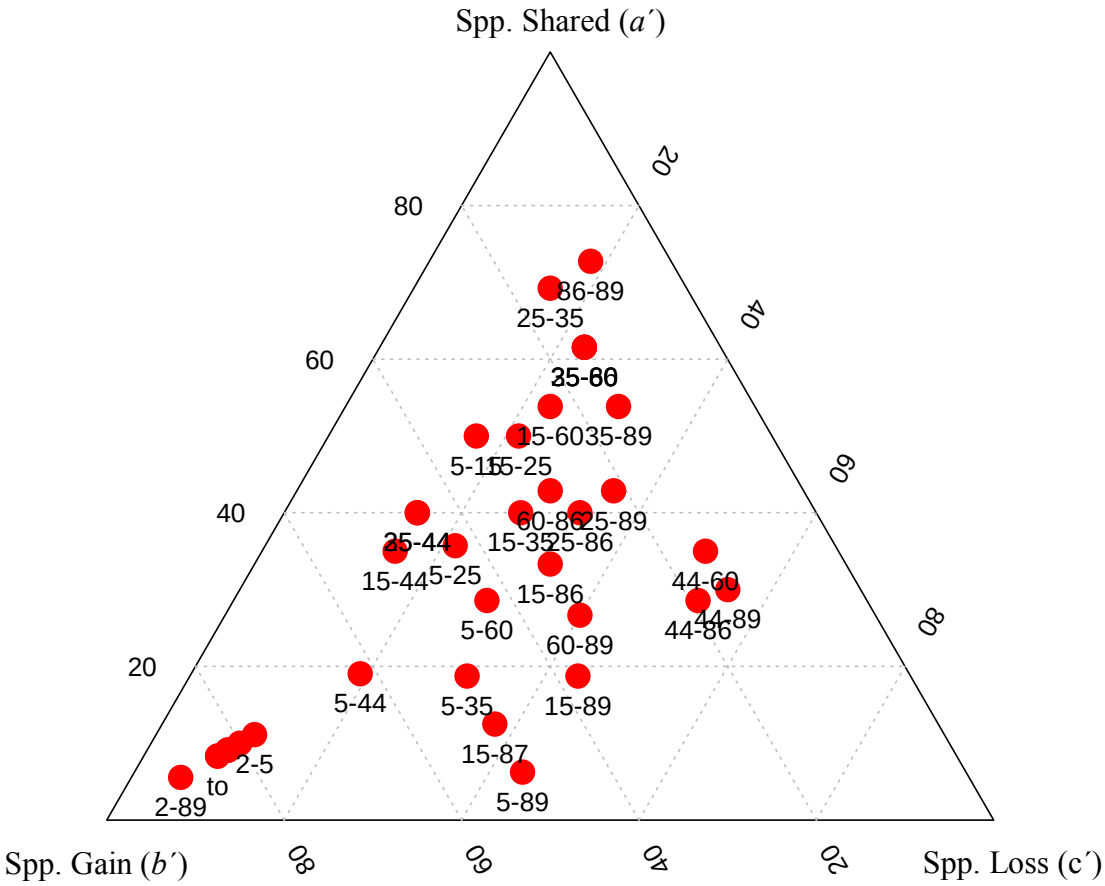


Figure 7. Ternary plot of pairwise age comparisons of Jaccard similarity from woody species presence/absence data collected across a chronosequence of *Pinus* plantations aged 2–89 years old, located in Kinleith Forest, central North Island, New Zealand. *Pinus* stand ages shown as numerals.

3.3.6. Species Composition

The *Pinus* chronosequence comprised a total of 29 species of trees, tree ferns, and shrubs (Appendix A). The shade-tolerant mature forest canopy and emergent species, namely: *B. tawa*, *H. arborea*, *K. excelsa*, *Litsea calicaris* (Lauraceae), and *W. racemosa*, were present in some mature *Pinus* plantations, particularly in the 44-year-old stand where indigenous forest was in close proximity (Fig. 8). Including the planted pines, four species were exotic. The indigenous forest reference site featured eight additional woody species that were not found in the *Pinus* chronosequence. However, fewer plots were measured in the indigenous forest (four plots), which potentially underestimates species richness when compared to the plantations where sampling was more extensive (32 plots). Species composition differed significantly among ($F9,29 = 8.921$, $P = 0.001$, $R^2 = 0.73$) but not within ($F9,29 = 0.687$, $P = 0.715$), the *Pinus* and indigenous forest stands (Fig. 8).

Changes in species composition over the first 15 years of the chronosequence were distinguished by the gain and subsequent loss of the light-demanding colonising species: *Coriaria arborea* (Coriariaceae), *Aristotelia serrata* (Elaeocarpaceae), and *Buddleja davidii* (Scrophulariaceae; exotic; Table 5; Fig. 8). Between 15 and 25 years, the increased abundance of the tree fern *D. squarrosa* was the most distinguishing floristic change, along with the increases in the abundance of the indigenous tree species: *Schefflera digitata* (Araliaceae) and *Coprosma robusta* (Rubiaceae). Further accumulation of indigenous forest tree and tree fern species was apparent over the period 25–35 years. Most notable from the SIMPER analysis were the gains in abundance of *M. ramiflorus*, *C. medullaris*, and *B. repanda*. *Hedycarya arborea* was the most dominant tree in the indigenous forest reference site and was a distinguishing feature of the 44-year-old *Pinus* stand. The composition of the oldest *Pinus* stand was most clearly distinguished from the indigenous forest reference site by the absence of *H. arborea* and the high abundance of both *D. squarrosa* and *P. arboreus*. The 35- and 44-year-old *Pinus* stands were closest in ordination space to the indigenous forest reference site (Fig. 8).

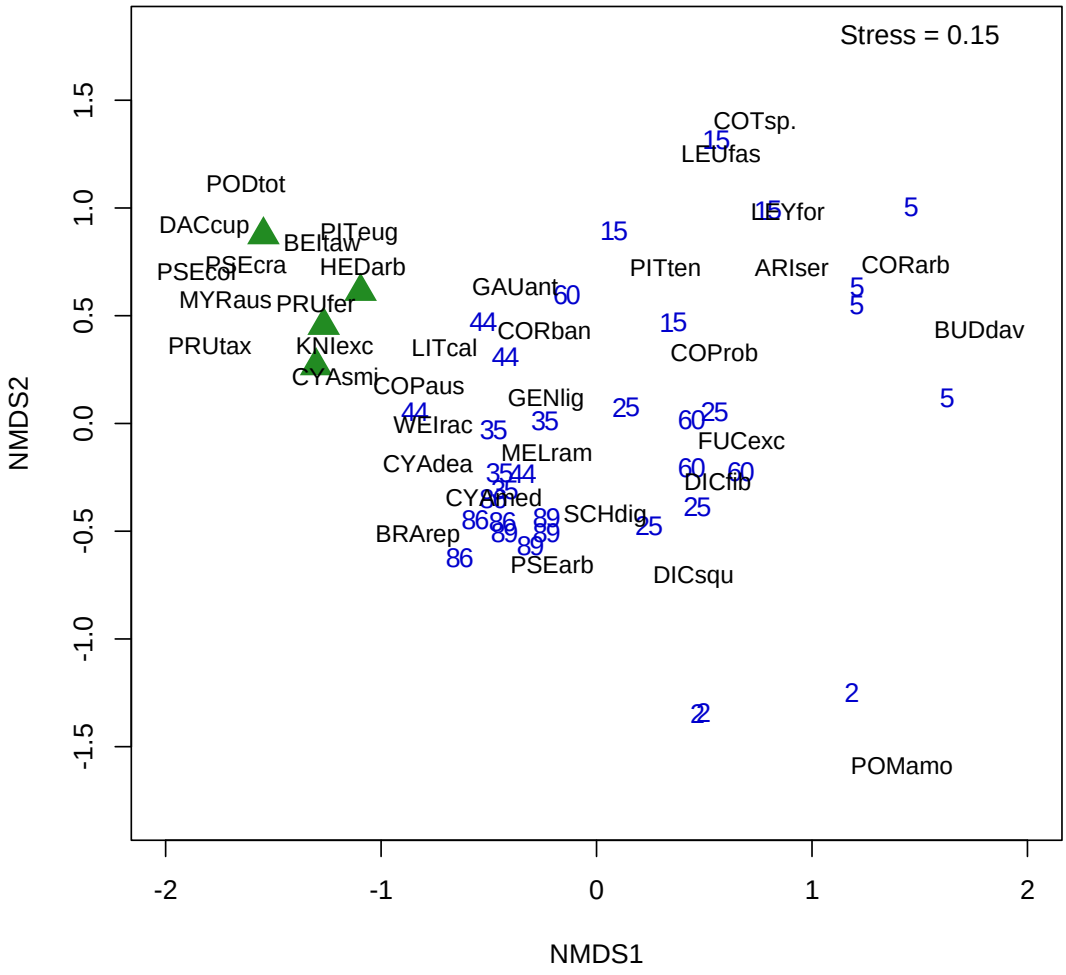


Figure 8. Nonmetric dimensional scaling (nMDS) ordination of species composition across chronosequence of nine *Pinus* plantation stands aged 2–89 years, Kinleith Forest, central North Island, New Zealand. The composition of an old-growth natural forest reference site is also included, shown by triangles. Six letter species codes are described in Appendix A.

Table 5. Similarity percentage (SIMPER) analysis of species composition from a chronosequence of nine plantation stands ranging in age 2–89 years located in Kinleith Forest, central North Island, New Zealand. The three species discriminating most between consecutive stand ages (% Contribution = "Contr."), and the cumulative percentage discrimination ("Cum.") are given. Old-growth natural forest ("NF") reference site included.

Species	Stand age																	
	2-5		5-15		15-25		25-35		35-44		44-60		60-86		86-89		89-NF	
	Contr.	Cum.	Contr.	Cum.	Contr.	Cum.	Contr.	Cum.	Contr.	Cum.	Contr.	Cum.	Contr.	Cum.	Contr.	Cum.	Contr.	Cum.
CORarb	**26±7**	**29**	16±4	22														
ARIser	**22±14**	**52**	14±8	40														
BUDdav	**15±13**	**69**	9±6	52														
DICsqu					**16±7**	**23**					**7±4**	**25**	6±4	36	**5±3**	**29**	11±3	30
SCHdig					**9±1**	**36**												
COProb					**8±3**	**49**												
MELram							**10±4**	**17**	6±2	13								
CYAmed							**7±4**	**30**			10±3	15	**8±6**	**27**	5±3	40		
BRArep							**6±5**	**41**	5±4	25			**11±5**	**16**	7±4	16		
HEDarb									**5±2**	**35**	6±2	35					**13±5**	**16**
PSEarb																	8±3	40

Note. Numerals in bold signify a gain in abundance, non-bold signifies a loss in abundance, underlined signifies no change in abundance. Species codes are given in Appendix A.

3.4. DISCUSSION

3.4.1. Forest Regeneration Processes

As predicted, we found that the structure and composition of *P. radiata* understories were strongly influenced by stand age and proximity to indigenous forest. Over the first 15-year period, conditions were most suitable for the light-demanding colonising species such as *C. arborea*, *A. serrata*, and the exotic *B. davidii*. Then as *Pinus* canopy cover and shade increased, these species were replaced by generalist forest tree species with greater shade tolerance, such as *S. digitata, M. ramiflorus,* and *B. repanda*. Although these are relatively early-successional species, they do have the ability to form a forest canopy. Although not the focus of this study, the successional direction observed is consistent with the acquisition of traits associated with later-successional species. Through the chronosequence there was a shift towards species with larger seeds, greater stature, and greater longevity (Weiher et al., 1999).

Stand age was a significant predictor of *S*. Where indigenous forest cover was in close proximity, we found both a greater density of indigenous woody seedlings and a greater abundance of mature forest canopy species, of closer compositional similarity to indigenous forest. This result was most apparent in the 44-year-old stand, where areas of indigenous forest were as close as 260 m from the sample plots and both species richness and woody seedling density were the highest of any of the plantation ages. The 44-year-old stand had a northern aspect and silty loam soils, and these attributes might also have assisted the establishment and growth of woody indigenous forest species. In the absence of replicated stand ages, we are unable to generalise our findings from the 44-year-old stand. Rather, we propose proximity to indigenous forest would be a significant predictor of both indigenous woody species richness and structure. Further research is required to investigate the role of proximity to indigenous forest on understorey regeneration patterns in *P. radiata* plantations.

In addition to the generalist shade-tolerant forest tree species, larger-fruited, bird-dispersed species such as *B. tawa*, *H. arborea*, and *L. calicaris* were found in high abundances in the 44-year-old stand. Yet, these species were either in low

numbers or were absent from stands of greater age. This finding supports our expectations that stand age is important from the perspective of creating shaded conditions for the establishment of shade-tolerant species. However, we suggest that proximal indigenous forest is required for the consistent natural establishment of larger-fruited, bird-dispersed mature forest canopy species in *P. radiata* plantations.

Our findings regarding the importance of stand age and the proximity to indigenous forest are consistent with existing national (Brockerhoff et al., 2003; Allen et al., 1995) and international literature. In the wet tropics of northern Queensland, Australia, *P. caribaea* plantations aged 5–31 years showed a significant increase in tree species richness with age ($R^2 = 0.788$), and 10–50-year-old *P. caribaea* plantations supported a total of 45 species of indigenous trees and shrubs, with the proportion of later-successional species increasing with age (Keenan et al., 1997). In the temperate Ethiopian Highlands, seed dispersal from adjacent areas of natural forest was identified as being important to enable incorporation of later-successional species into the understories of *P. patula* plantations (Senbeta et al., 2002).

Of New Zealand's *ca*. 240 woody plant species, about 70% are bird dispersed (Clout & Hay, 1989), and of the 21 tree and shrub species surveyed from the *Pinus* chronosequence, 16 (76%) were dispersed by birds. Aside from less frequent long-distance dispersal, effective bird dispersal operates over typically short distances in New Zealand. Wotton and Kelly (2012) found that mean dispersal distance of *B. tawa* by New Zealand Pigeon (*Hemiphaga novaeseelandiae*) was 95±171 m. Only 21% of seeds were dispersed > 100 m, and only < 1% of seeds were dispersed > 1000 m. We found numerous seedlings of *B. tawa* in the 44-year-old *P. radiata* understorey located close to indigenous seed sources, while *B. tawa* was scarce or absent from understories of more isolated stands. New Zealand Pigeon is the only extant bird species capable of dispersing *B. tawa*'s large fruit (Clout & Hay, 1989). Given the presence of *B. tawa*, and considering the species dependence on New Zealand Pigeon for seed dispersal, we can conclude that the dispersal of *B. tawa* was by frugivory from adjacent natural forest, and therefore that bird dispersal was operational at the 44-year-old stand, where species richness and seedling densities were greatest.

Studies of the ubiquitous European blackbird (*Turdus merula*) have also shown that most seeds are dispersed by this species within only 50 m, while some might be spread up to 1 km or more (Williams, 2006). Nectar-feeders and frugivores are major components of New Zealand's avifauna, and given the *Pinus* genus does not provide nectar or fruit resources, important insectivorous and frugivorous dispersers are only sometimes present in *P. radiata* plantations (Clout & Gaze, 1984). Therefore, the presence of mature indigenous vegetation in the surrounding landscape matrix is important for both the presence of indigenous dispersal vectors and the availability of indigenous forest propagules, this importance is reflected in our results.

We predicted that the relatively light-demanding podocarp species would not be present in mature *P. radiata* plantations due to either heavy shading or ecological isolation from indigenous forest seed sources. Even where mature indigenous forest was proximal, we found no conifer species, and while this makes it difficult to confirm the reasons for their absence, possible explanations are found in the existing literature. Initiation of the regeneration of New Zealand's long-lived podocarps is disturbance related, insofar as a competitive release is required for the successful establishment and growth of seedlings (Carswell et al., 2012; McKelvey, 1963).

Therefore, it is plausible that if seeds were dispersed to *P. radiata* plantations, these conifer species would benefit from the disturbance of both the homogenous plantation canopy and any dense understorey growth, to increase understorey light levels and stimulate podocarp seedling growth. We note however, both *P. ferruginea* and *P. taxifolia* have been found to inhabit multiple mature *P. radiata* plantations across New Zealand, suggesting that it is sometimes possible for these podocarp species to establish themselves within mature *P. radiata* plantations (Brockerhoff et al., 2003). Podocarp dispersal is dependent on frugivory (Beveridge, 1964), so in our study the absence of podocarps in the *P. radiata* chronosequence might also be attributed to the fragmented nature of the surrounding indigenous forest landscape, and to a general scarcity of podocarp seed sources in proximity to mature *P. radiata* stands.

Existing studies have identified two reasons for compositional differences between mature *P. radiata* stands and natural forest: Insufficient stand age required to

provide conditions suitable for regeneration requirements to be met (Onaindia et al., 2013), and ecological isolation (Onaindia et al., 2009). Interventions to create more heterogeneous light conditions in *P. radiata* plantations might assist with the recruitment of missing mature forest tree species (Onaindia et al., 2013). There are grounds to expect canopy interventions or understorey manipulations would benefit podocarp establishment and seedling growth in mature *P. radiata* plantations.

Our results strongly suggest that birds were dispersing indigenous forest seeds into the 44-year-old stand, although we are unable to determine whether podocarps were present in the seed rain, nor are we able to confirm whether light levels were suitable for podocarp establishment and growth. However, sufficient stand age, proximal indigenous forest sources, and suitable light levels such that might be created by canopy gaps are all probable prerequisites for the reliable establishment of New Zealand's long-lived podocarps in *P. radiata* plantation forests.

The scarcity of mature forest canopy species colonising mature *P. radiata* plantations, and in particular isolated *P. radiata* sites, has implications for the composition of future forests at these sites. We consistently found generalist tree species colonising mature *P. radiata* understories, such as *B. repanda*, *P. arboreus*, *P. tenuifolium*, *S. digitata*, *M. australis*, and *M. ramiflorus*. The *P. radiata* understories also featured a high density of tree ferns of the Cyatheaceae and Dicksoniaceae families. Where mature forest seed sources were proximal, we found the mature forest canopy species *B. tawa*, *H. arborea*, *K. excelsa*, and *L. calicaris*. However, even in those instances, we found no podocarps. This absence of podocarps in vegetation communities of similar ages to our *Pinus* stands is consistent with the findings from studies of podocarp regeneration in indigenous broadleaved forest. Where a podocarp seed source is available, a nurse crop of broadleaved angiosperms, or *Leptospermum scoparium* (Myrtaceae) or *Kunzea* spp., is normally required for podocarps to establish themselves. In these natural successions the development of nursery conditions suitable for podocarp establishment is known to take 30–60 years or longer (Cameron, 1960; McKelvey, 1955).

These results suggest that, at ecologically isolated stands, the future forest composition would be dominated by shorter-statured species with relatively short life

expectancy, and that these forests would be distinguished from nearby natural tall forests by the absence of characteristic, very-long lived, old-growth forest canopy species, such as *B. tawa* and *D. cupressinum*. Where mature forest canopy species were present in higher densities due to the close proximity to natural forest, the presence of species such as *B. tawa*, *H. arborea*, and *K. excelsa* provide an indication of convergence towards natural forest composition. However, the absence of podocarps means that a major compositional component of intact natural forests appears to be missing. Where attainment of natural forest composition is the restoration objective, these results suggest that management interventions might be required to direct the regeneration processes operating in mature *P. radiata* stands, in order for the stands to be more representative of natural forest.

3.4.2. Considerations When Managing Non-Harvest Stands as Restoration Sites

Although our results provide further support for the role that *P. radiata* plantations play as a facilitative nurse crop, we identify some potential factors that may act to influence indigenous regeneration processes in *P. radiata* stands. Understanding the nature of these influences is important where non-harvest *P. radiata* stands are to be managed for the purposes of restoring indigenous forest cover.

Even-aged monoculture plantations are usually initially low in structural diversity and this may limit understorey plant species richness (Gamfeldt et al., 2013), recruitment of future canopy tree species on the site (Royo & Carson, 2006), and the potential of wider forest biodiversity values (Lindenmayer et al., 2006). Heterogeneity in canopy cover through formation of canopy gaps, or variation in the vertical structure of the forest may take an extended period of time to develop naturally (Kuuluvainen et al., 2002; Lust et al., 1998). In particular, we note that interventions mimicking the effects of disturbance, such as the creation of artificial canopy gaps, are likely to benefit the establishment and growth of podocarps. For these reasons, we suggest that early interventions such as the creation of small-scale artificial canopy gaps to increase canopy heterogeneity may provide important opportunities to maximize the biological diversity of exotic *P. radiata* plantations.

In addition to the competitive shading effects of the plantation canopy, after several decades, additional competitive effects may result if very dense understorey growth develops (Royo & Carson, 2006), such as heavily shading herbaceous or fern dominated understories (De la Cretaz & Kelty, 2002). This result might mean that even if *Pinus* canopy openness increases with age, secondary competitive effects from a dense understorey will still limit forest floor regeneration processes. In the understories of mature Spanish *P. radiata* plantations, species from the genera *Rubus* and *Graminae* grew rapidly, demonstrating fast lateral spread, achieving dominance and, as a result, were highly competitive on forest floor regeneration processes. Management interventions were recommended to address these competitive effects on forest regeneration (Onaindia et al., 2013). We found that adult tree ferns entered the chronosequence between 15 and 25 years and continued to increase in dominance over the next 50 years or more, reaching densities of 1125±433 stems ha^{-1}. Ogden et al. (1997) also found the understorey composition in older *P. radiata* stands to be dominated by tree ferns (tree fern stem densities of 2000–3000 stems ha^{-1}). In such conditions, the same competitive shading effects that have been reported from New Zealand's indigenous forests (Gaxiola et al., 2008; Coomes et al., 2005; Newton & Healey, 1989) may apply, limiting regeneration processes in these exotic plantation forests.

However, we found a positive aspect to tree fern dominance. In stands older than 44-years epiphytic establishment of indigenous woody trees occurs. Woody epiphytes were in greater abundance in lower-density tree fern stands. In dense forest, most seedlings of the light-demanding canopy dominant *W. racemosa* are epiphytic, and these can be numerous on tree fern trunks (Wardle & MacRae, 1966). We therefore suggest that thinning tree fern stands to retain tall specimens, with reduced shading from adjacent tree ferns, will provide a means of reducing competitive interactions, thereby increasing opportunities for regeneration of indigenous woody species in these planted forests.

Where the natural dispersal of old-growth forest canopy species is limited, their active introduction might be required. Within Kaingaroa Forest, a large commercial exotic plantation forest also located in the central North Island of New Zealand, we found that underplanting of podocarps under a degraded *Pinus ponderosa* canopy

accelerated forest succession by establishing the structural dominance of a long-lived mature forest canopy species within only 50 years (Forbes et al., 2015). Similar interventions involving the underplanting of non-harvest plantation understories to incorporate late-successional species have also been successful in Sri Lankan (Ashton et al., 1997), Spanish (Rodriguez-Calcerrada et al., 2008), and German (Noack, 2011) *Pinus* plantations.

3.4.3. Implications for Biodiversity Conservation in New Zealand

The exotic *P. radiata* canopy facilitates a regeneration trajectory characterized by shade-tolerant indigenous forest species. Our results show that, even at ecologically isolated sites, the microclimate conditions created by plantation *Pinus* stands can support a suite of readily-dispersed indigenous forest plants. The structural and compositional aspects of indigenous forest regeneration in older *P. radiata* stands are broadly comparable to New Zealand's mid-successional natural forest communities (Ogden et al., 1997; Allen et al., 1995); and are superior in comparison to exotic pastoral landscapes, where indigenous forest species are typically restricted in distribution to degraded remnant habitat patches or to scattered or solitary remnants, or have become locally extinct (Brockerhoff et al., 2008b; Norton & Miller, 2000). Our results emphasise the importance of maintaining indigenous cover in production landscapes (Craig et al., 2000), and show how the benefits of doing so can extend beyond the boundaries of those indigenous communities, by boosting biodiversity values in adjacent exotic planted forests (Carnus et al., 2006). Non-harvest *P. radiata* stands provide an important opportunity for the restoration of indigenous forest communities in New Zealand's production landscapes. However, although where restoration of mature forest composition is the restoration objective, interventions might be necessary to direct and accelerate the secondary forest succession.

4. CHAPTER THREE:

Artificial Canopy Gaps Accelerate Restoration Within an Exotic *Pinus radiata* Plantation

CHAPTER PREFACE

Chapter Two concluded that the understorey light environment is an important predictor of understory regeneration patterns, and that understorey light levels are modified by vegetation cover, in particular through age-related stand structural changes. Chapter Two also established that even-aged monoculture plantation canopies are usually initially low in structural diversity, and that this structural homogeneity might constrain understorey regeneration processes. Through Chapter Two it was also found that podocarps were not establishing in *P. radiata* understories, even when indigenous forest cover was proximal. It was suggested that the usually light-demanding podocarps normally require a disturbance to release them from competition, and that this influence is essentially missing from young managed *Pinus* plantation stands, and without intervention such canopy heterogeneity might take an extended period to develop.

Chapter Three develops these findings from Chapter Two, principally that the understorey light environment is a critical predictor of patterns in forest understorey regeneration. Here, experimental small-scale canopy gaps are trialled as a means of accelerating growth rates of two mature forest canopy species planted within *P. radiata* plantation forest. Through this canopy gap experiment, Chapter Three addresses the issue of competitive shading by the *Pinus* canopy, and provides insights into the corresponding constraints of canopy structural homogeneity on understorey regeneration.

Chapter Three has been published in the journal Restoration Ecology. My Supervisors, Prof. David Norton and Dr. Fiona Carswell, are co-authors of the manuscript. This paper is enclosed as Appendix B, and the citation for the paper is:

Forbes, A. S., Norton, D. A., & Carswell, F. E. (2015). Artificial canopy gaps accelerate restoration within an exotic *Pinus radiata* plantation. *Restoration Ecology*. Advance online publication. doi: 10.1111/rec.12313

4.1. ABSTRACT

We created small-scale artificial canopy gaps to accelerate the growth of mature indigenous forest canopy species for restoration of an 18-year-old exotic *Pinus radiata* plantation forest, in the Marlborough Sounds, New Zealand. Small and large circular gaps were formed by felling. Seedlings of two indigenous forest canopy species, *Podocarpus totara* (Podocarpaceae) and *Beilschmiedia tawa* (Lauraceae), were planted within artificial gaps and undisturbed plantation canopy. Seedling height growth, mortality, and occurrence of animal browse were monitored at approximately 6-month intervals over 17 months.

Both *P. totara* and *B. tawa* differed significantly in height growth and in animal browse occurrence among artificial gap treatments. Growth of the light-demanding *P. totara* was better under large canopy gaps, whereas growth of the shade-tolerant *B. tawa* increased under gaps of any size but was most consistent under small gaps. For *P. totara*, any significant restoration benefit of gap formation on height growth was lost when browsed seedlings were taken into account. Animal browse significantly limited *B. tawa* height growth in large but not in small gaps.

Small-scale canopy gap creation is an effective method of modifying light transmission to the plantation understorey and accelerating seedling growth rates. Canopy gap size can be used to optimise the understorey light environment according to species-specific light requirements. The increased occurrence of animal browse in gaps require consideration. Artificial canopy gaps within planted monocultures creates structural heterogeneity that would otherwise take an extended period of time to develop. These results further support the role of plantations as indigenous forest restoration sites.

4.2. INTRODUCTION

Plantation forests are recognised globally as potential sites for the restoration of indigenous forest communities (Carnus et al., 2006; Lamb et al., 2005; Lamb 1998). Plantation trees are often established on sites with limited opportunities for economic returns, and plantation owners may be more interested in using the plantation stand to facilitate an indigenous secondary forest succession for biodiversity restoration (Lamb et al., 2005). The facilitative role exotic plantation forests can play in the recruitment of indigenous forest species has been widely studied (e.g., Brockerhoff et al., 2008; Carnus et al., 2006; Lugo 1997). In particular, shelter associated with plantation canopy closure may ameliorate climatic conditions (e.g., frost, desiccation) at open sites that would otherwise prevent indigenous canopy tree seedlings from establishing (Carnus et al., 2006; Brockerhoff et al., 2003; Cannell 1999).

However, plantation canopy cover usually increases to a point where excessive shade limits the establishment and growth of indigenous woody species, especially those species that will form the eventual canopy (Yirdaw & Luukkanen, 2004). In the absence of intervention, most plantation canopies will persist for many decades before the canopy opens sufficiently (through mortality and gap formation) to result in light transmission characteristics suitable for recruitment of indigenous forest canopy species. Delayed successional development due to shade is particularly the case within *Pinus* plantations in temperate climates, where an indigenous dominated understorey composition can take 15–20 years to develop, and even then comprises predominantly shade-tolerant understorey species (Brockerhoff et al., 2003; Ogden et al., 1997; Allen et al., 1995). Several more decades may then be required before light conditions are suitable for the establishment of indigenous forest canopy species.

Therefore, where exotic plantation managers seek to accelerate a transition toward indigenous forest dominance, methods to optimise understorey light conditions for the early incorporation of indigenous canopy tree species in the forest succession are highly desirable, particularly in relatively young plantations when both the canopy density and the degree of canopy light interception can be high. In addition to limitations imposed by shading, the natural establishment of indigenous canopy species within plantations may not occur due to a lack of either propagule

availability or dispersal (Duncan & Chapman, 2002). Underplanting plantation stands with mature forest canopy species is a method of overcoming dispersal limitation. However, attainment of specific understorey light conditions is required in order for planted species to thrive in the plantation understory (Forbes et al., 2015).

Forest canopy gaps serve a critical role in influencing understorey light regimes (Canham et al., 1990). Plantation and restoration managers can stimulate forest succession by creating artificial canopy gaps, mimicking the effect of natural disturbance events on canopy structure and understorey light regimes (Lamb et al., 2005; Lindh & Muir, 2004). This approach is underpinned by the Gap Partitioning Hypothesis (see: Denslow 1980; Ricklefs 1977), which predicts that species with contrasting life history strategies are able to co-exist along resource gradients, such as the resource gradient that exists from intact forest canopy through to the centre of a forest canopy gap. Of particular relevance, Ricklefs (1977) suggests that young individuals of tree species will be distributed according to soil and micro-environmental gradients, and when gradients of these two parameters are produced experimentally (e.g., canopy gap creation), distinct responses will be evident, with different species having their own specific gap requirements.

A number of studies have investigated the role of canopy gap creation within *Pinus* (Pinaceae) plantation stands for restoration of indigenous forest communities. Removal of consecutive rows of *Pinus caribaea* in Sri Lanka created different widths of canopy opening strips (4 and 8 m) and resulted in differences in height growth of planted tropical late-successional forest trees (Ashton et al., 1997). Canopy gap creation in boreal *Pinus sylvestris* plantation forest in Finland by scaling experimental canopy gap treatments to canopy tree height (gaps ranged 3–20 m dia.) was found to advance the existing dominant species of the gap understorey, thereby contributing toward restoration goals (Rouvinen & Kouki, 2011). In Japan, circular canopy gaps were used to promote forest succession from the understorey of a 40-year-old *Pinus thunbergii* plantation, with gap size the main factor affecting seedling growth and both growth and establishment being greatest in large gaps (Zhu et al., 2003). Results from these studies are consistent with the Gap Partitioning Hypothesis, insofar as the growth performance of forest tree seedlings within artificial canopy gaps is dependent

on both the specific gap light environment (governed principally by gap size) and the respective species life history strategy regarding tolerance of shade.

We suggest that exotic *Pinus* plantations can be used to overcome existing barriers to indigenous forest restoration. In particular, we propose that non-harvest *Pinus* plantations provide shelter to allow canopy trees to regenerate in association with minor canopy manipulations (Forbes et al., 2015; Norton & Forbes, 2013). In central New Zealand, we assessed the potential of small-scale canopy gap interventions within relatively young *Pinus radiata* (Pinaceae) plantations to enhance growth of seedlings of two indigenous mature forest canopy tree species, *Beilschmiedia tawa* (Lauraceae), and *Podocarpus totara* (Podocarpaceae). We expect these results to provide insights into the potential use of artificial canopy gaps when restoring non-harvest *P. radiata* plantations, and these results may then be adapted to *P. radiata* plantations in other localities where the restoration of locally relevant indigenous canopy dominants is desired. *Beilschmiedia tawa* and *P. totara* have contrasting shade tolerances. *Beilschmiedia tawa* is a highly shade-tolerant species (Lusk et al., 2009; Smale et al., 2008; Smale & Kimberley, 1986) and its seedlings are both shade-tolerant (Burrows, 1999) and sensitive to exposure (Knowles & Beveridge, 1982). *Beilschmiedia tawa* has the ability to regenerate effectively both in small gaps and under a closed canopy (Smale & Kimberley, 1983). These observations suggest that small canopy gaps will be of most benefit to *B. tawa* regeneration. In contrast, *P. totara* is light demanding and has a rapid growth response to canopy opening (Ebbett & Ogden, 1998). *Podocarpus totara* is known to regenerate most vigorously in high-light environments such as large windthrow gaps and forest margins, among open scrub (McSweeney, 1982), and even in grazed exotic grassland (Bergin & Kimberley, 2014).

We hypothesise that the creation of canopy gaps within an 18-year-old *P. radiata* plantation increases light transmission to the forest understorey, which then stimulates height growth of planted seedlings of two indigenous canopy species with contrasting ecologies. We investigated the effect of different sized circular canopy gaps, hypothesising that larger gaps would provide more favourable conditions for growth of the light-demanding species – *P. totara*, whereas smaller gaps would provide better conditions for growth of the more shade-tolerant species – *B. tawa*.

4.3. METHODS

4.3.1. Study Area

Located in a coastal position in the Marlborough Sounds, in the northeast of the South Island of New Zealand (41°39'37"S 174°06'15"E), the study area has a mild humid climate (Laffan & Daly, 1985) and receives a high number of sunshine hours per year (1948–2014 annual average = 2289 sunshine hours). The annual average (1941–2014 average) temperature is 13°C, and monthly average temperatures range from 18°C (February) to 7°C (July). Frosts occur rarely and are usually only light (N. Guard 2015, adjacent landowner and resident, personal communication). The annual average (1968–2000 average) rainfall is 1411 mm, with monthly rainfall varying from 84 mm (February) to 146 mm (July). Soil moisture deficits can occur during the summer months. Sunshine and temperature statistics were measured at the Blenheim Climate Station, located *ca*. 23 km to the southwest of the site. All other climate data were measured at the Ocean Bay Climate Station, located *ca*. 1 km to the south of the site (National Institute of Water and Atmospheric Research [NIWA], 2014).

The site is located on north-facing, steeply sloping hill country at an elevation range of 40–120 m above sea level (a.s.l.). Soils are well-drained, formed from siliceous parent materials with silty clay to silty clay loam texture, and are of low nutrient status (Walls & Laffan, 1986). The underlying geology is weakly metamorphosed Marlborough Schists grading down from Pelorus Group indurated sandstone and siltstone (Beck, 1964).

The coastal broadleaved forest that covered the site prior to European settlement would have been dominated by the angiosperm trees *B. tawa*, *Elaeocarpus dentatus* (Elaeocarpaceae), and *Dysoxylum spectabile* (Meliaceae), with lesser numbers of *Weinmannia racemosa* (Cunoniaceae) and *Fuscospora fusca* (Nothofagaceae) (Walls & Laffan, 1986). Podocarpaceae species, including *P. totara*, would have been present as scattered emergent trees through this forest (Walls & Laffan, 1986). However, since the late 19th Century, much of the wider study area has been cleared of natural forest for pastoral farming (Laffan & Daly, 1985). More recently, commercial exotic plantation forestry, principally using *P. radiata*, has replaced

pastoral agriculture on many of the hill regions within the eastern Marlborough Sounds.

Several introduced mammals are present in the study area, including *Dama dama* (fallow deer) and a small number of *Cervus elaphus scoticus* (red deer) (J. Guard 2013, adjacent landowner and resident, personal communication) *Sus scrofa* (feral pig) were observed within the experimental site over the course of the study, as were faecal pellets of *Trichosurus vulpecula* (brushtail possum). *Lepus europoeus occidentalis* (brown hare) may also occasionally be present.

4.3.2. Experimental Design

The effect of increased light transmission on indigenous seedling height growth was tested through the creation of two sizes of circular canopy gaps within an 18-year-old (at 2013) *P. radiata* plantation. The 18-year-old stand represented closed-canopy conditions, where successful intervention would allow early incorporation of mature forest tree seedlings within the forest succession. The experimental forest stand was the first rotation of planted *P. radiata* on the site and was thinned to waste at 14 years of age. Prior to the plantation establishment, an exotic shrubland occupied the site, having established itself on abandoned pasture. When the experiment was established the *Pinus* stand had a mean top height of 24.0 m (± 0.5, $n = 91$), a mean stem diameter (DBH) of 31.7 cm (± 0.5, $n = 272$), a mean stem density of 831.9 trees ha^{-1} (± 92.1, $n = 22$), and a mean basal area of 49.5 m^2 ha^{-1} (± 2.5, $n = 22$).

We selected plot locations at random points using the geographic information system (GIS) ArcMap 10.1 (ESRI, 2011), and then we assigned treatments to plots on a random basis. All experimental plots were contained within a *ca*. 22 ha area of plantation forest. To avoid edge influences, plots were not located within a 20 m exclusion buffer around the plantation edge, although the closest plot to this edge was 40 m distant. Interference between plots was avoided by the imposition of a minimum 22 m separation between plot centres, although all plot separation distances were well in excess of this minimum distance. The GIS-derived plot coordinates were located in the field, using a hand held global positioning unit (Garmin GPSmap 62s).

In total, seven small gap treatments, eight large gap treatments, and eight control (unmodified *Pinus* canopy) plots were established. During the course of the experiment, one large treatment plot was heavily browsed by stock entering from an adjacent paddock, and seedling data from that plot were excluded from subsequent analyses. All *P. radiata* trees occurring within either a 2.3 m (small gap) or 5.6 m (large gap) radius of the plots' centre points were felled to create circular canopy gaps. The final expanded canopy gap diameter (Runkle, 1982) extended to the next nearest tree, resulting in final gap diameters wider than the measurements that were used to initially select trees for canopy gap creation. The two gap sizes aimed to mimic what might be formed naturally from small-scale disturbance resulting from events such as canopy tree mortality or windthrow. The forest canopy was not disturbed in the control plots.

Forest canopy structure and understorey light environment were quantified at all plots using 180° hemispherical (fisheye) photography. The effect of canopy opening treatments on the understorey light environment was quantified through measurements undertaken before and after canopy modification. Hemispherical photographs were taken from 1.35 m above ground level (a.g.l.) at plot centres, using a Pentax K200 DSLR fitted with a Sigma 4.5 mm circular fisheye lens.

Expanded gap diameter to height ratios (gap ratios) were determined by taking the average of two orthogonal expanded gap diameters divided by the average top height of four gap-edge boarding *P. radiata* trees. Plot exposure was assessed by calculation of Mesoscale Topographic Index, the mean of eight equidistant slope to horizon measurements measured at the plot centre, following McNab (1993). *Pinus* canopy height was measured using a Geosystems Vertex III hypsometer. Stand basal area was determined using a basal area prism (Factor 4) by multiplying the prism-derived stem count by four (the prism multiplier). Diameter at breast height (dbh) was measured at 1.35 m (a.g.l.).

Within each of the 23 plots, 12 *B. tawa* and 12 *P. totara* nursery-raised potted seedlings were planted in an alternating grid pattern at 30 cm spacing during August 2013. The planted seedling grid was centred on the gap centre point. This coincided with the point from which the hemispherical photograph was taken, and allowed us to

relate canopy architecture and gap light transmission results to seedling performance results. Given the moderate to slow growth rates of these mature canopy species, their relatively sparse foliage cover, and the seedling heights at the start and end of the experiment, we believe the 30 cm spacing among seedlings was sufficient to avoid above or belowground competition among seedlings. Seedling height, mortality, and occurrence of animal browse were monitored at approximately 6 monthly intervals over the following 17 months.

Any shade-induced apical die-back represented part of the intrinsic seedling growth performance among gap treatments, and therefore seedling height measurements were always taken at the highest live apical point. To separate the intrinsic growth rate data collection from growth rate data affected by animal browse, seedlings affected by animal browse were recorded as having been browsed for the reminder of the experiment. The total seedling growth increment and the proportions of both browse occurrence and seedling mortality were calculated once at the conclusion of the experiment. Therefore, these results represent seedling growth performance, the proportional occurrence of animal browse, and seedling mortality over 17 months.

Any natural establishment of exotic herbaceous plants within experimental plots was controlled by hand weeding over the duration of the experiment. This eliminated the potential for any competitive effects by exotic herbaceous coloniser species on planted seedling growth.

4.3.3. Statistical Analysis

Differences in slope aspect among experimental plots were assessed using functions of the R (R Development Core Team [R], 2014) Circular package, and probability values were calculated using the Wallraff rank-sum test of angular distance, which comprises a usual Kruskal-Wallis rank sum test. Differences in mean slope and Mesoscale Topographical Index among treatments were assessed using Kruskal-Wallis rank sum test. Percentage canopy openness data were Logit transformed before differences among experimental treatments were tested using Wilcoxon rank-sum test. The experimental effects on proportional changes in light transmission were assessed using a Generalised Linear Model (GLM) applying the

Binomial family and default Logit link function. Post-hoc pairwise comparisons of significance were carried out for GLMs using the glht function of the R Multcom package.

Over the course of the experiment some seedlings were browsed by introduced mammalian herbivores, and we expect that this would have a confounding effect on seedling growth rates. In order to exclude the confounding effect of mammal browse on seedling growth rate results, we analysed the growth rates of "unbrowsed seedlings" for each species separately. The analysis of "unbrowsed seedlings" enabled us to analyse the intrinsic growth rates of the two species and avoid the confounding effect of mammal browse. We then carried out a second, separate, analysis of grouped "browsed" and "unbrowsed" seedling growth rate data for each species ("all seedlings combined"). This analysis of all seedlings combined provided an illustration of the net growth rate for each species when creating canopy gaps for restoration, in the presence of introduced herbivores.

Differences in mean seedling height at the time of experiment establishment were assessed using one-way ANOVA. The effect of experimental canopy gap treatments on "unbrowsed seedling" height growth was assessed using simple linear regression. The combined effects of canopy gap creation and the occurrence of mammalian animal browse on "all combined" seedling height growth were assessed using multiple linear regression. For inclusion in multiple regressions, the proportional occurrence of animal browse (explanatory variable) was Logit transformed.

Differences in the proportional occurrence of mammalian animal browse and mortality among experimental treatments were assessed separately using GLMs applying the Binomial family, with default Logit link function, or Quasibinomial family, with F-test when a model was over-dispersed. For *P. totara* mortality, due to unsatisfactory GLM diagnostics, Fisher's exact test was used to assess differences in the proportion of mortality among experimental treatments. All error estimates given are one standard error of the mean unless otherwise stated.

Seedling relative height growth (RHG) was calculated using the formula:

$$RHG = T2 - T1/T1 \qquad \textit{Equation 1}$$

where T1 and T2 were absolute seedling heights measured at the time of experiment establishment and 17 months later, respectively. Therefore, the RHG results represent the growth increment over a 17-month period.

The imaging software Gap Light Analyzer (GLA, Version 2; Frazer et al., 1999) was used to extract percentage canopy openness and light transmission data from hemispherical photographs. For GLA modeling, the growing season was defined as 1 September–31 March, the default solar constant used was 1367 Wm–2, and the Cloudiness Index, Spectral Fraction, and Beam Fraction were all set at 0.5.

4.4. RESULTS

Physical plot characteristics (Appendix C) among experimental treatments were similar. Mean slope values among experimental treatments were not significantly different (Kruskal-Wallis rank-sum, $H(2) = 4.57$, $P = 0.102$) and ranged from 18–29˚. Slope aspects were generally to the north, and mean slope aspect values did not differ significantly among treatments (Kruskal-Wallis chi-square, $H(2) = 3.01$, $P = 0.222$). Mesoscale Topographical Index values also showed sites were of similar exposure among treatments (Kruskal-Wallis rank-sum, $H(2) = 0.96$, $P = 0.618$).

4.4.1. Gap Characteristics and Gap Light Environments

Mean gap ratio scores differed significantly (one-way ANOVA, $F(2,20) = 65.41$, $P = < 0.001$) among intact forest canopy (control) (0.20 ± 0.01), small gap treatments (0.40 ± 0.03), and large gap treatments (0.58 ± 0.03). Differences among all treatments were all $P < 0.001$. Canopy gap creation significantly increased percentage canopy openness (Wilcoxon rank-sum test, $W(n_1 = 7, n_2 = 7) = 8$, $P = < 0.038$) at both small gap treatments (before = 14.4% ± 1.3; after = 18.2% ± 1.4) and large gap treatments (before = 14.6% ± 1.3; after = 25.6% ± 1.6), $t(7) = -5.988$, $P = < 0.001$) (Fig. 10A). Gap creation significantly increased the percentage of total light transmitted to the forest understorey (Generalised Linear Regression, $F(3) = 13.9$, $P = 0.003$), with significant ($\beta = 2.729$; $P = 0.031$) increases in light transmission resulting

from creation of large gaps (before = 25.1% ± 12.1; after = 83.7% ± 9.1) (Fig. 10B). Total light transmission increased as a result of small gap creation (before = 22.8% ± 10.3; after = 48.6% ± 12.4), although this increase was much less than that of large gap creation and was not statistically significant (β = 1.17; $P = 0.427$). Although not statistically significant, small gap creation was sufficient to effect considerable growth response in planted seedlings. Absolute total radiation (direct plus diffuse) over the growing season at 1.35 m (a.g.l.) differed significantly (one-way ANOVA, $F(4,33) = 7.979$, $P = < 0.001$) among gap treatments. In small gaps, absolute total radiation increased ($P = 0.086$) from 0.53 mol m^{-2} d^{-1} (± 0.15) to 1.13 mol m^{-2} d^{-1} (± 0.27); and in large gaps, radiation increased ($P = 0.001$) from 0.40 mol m^{-2} d^{-1} (± 0.04) to 1.33 mol m^{-2} d^{-1} (± 0.18). Significant differences occurred in total radiation between unmodified canopy 0.44 mol m^{-2} d^{-1} (± 0.06) and both small ($P = 0.027$) and large gaps ($P = 0.002$), respectively.

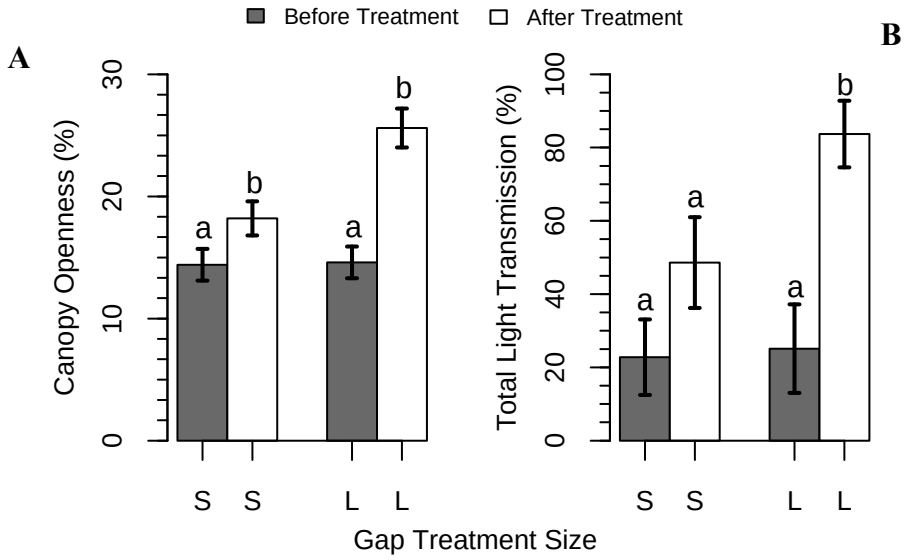


Figure 9. Mean forest canopy openness (%) and total light transmission (%) of two sizes of experimental canopy gap treatments (S = Small Gap (mean 9.4 m diameter (± 0.7 m)) & L = Large Gap (mean 14.6 m diameter (± 1.0 m))) before and after gap creation treatment, within an 18-year-old *Pinus radiata* plantation, Marlborough Sounds, New Zealand. Paired columns with coinciding letters indicate no significant difference, whereas column pairs with different letters indicate significant differences at $P < 0.05$. Error bars represent ±1 SE.

4.4.2. Seedling Growth Response and Occurrence of Animal Browse

Podocarpus totara

The initial mean absolute height of *P. totara* seedlings was 294.7 mm (± 7), and absolute seedling heights did not differ significantly among treatments (one-way ANOVA, $F(2,19) = 0.636$, $P = 0.540$). Seventeen months after gap creation, *P. totara* seedlings were significantly different among the gap treatments (one-way ANOVA, $F(5,32) = 5.275$, $P = 0.001$) (Fig. 11A). Mean absolute seedling heights by treatment were: "control unbrowsed" = 322.2 mm (± 12); "control all combined" = 322.1 mm (± 12); "small unbrowsed" = 358.8 mm (± 20); "small all combined" = 368.6 mm (± 16); "large unbrowsed" = 424.8 mm (± 27); "large all combined" = 397.7 mm (± 19). Unbrowsed *P. totara* seedlings under large gaps (0.52 ± 0.11 RHG) grew to approximately four times the height of either unbrowsed (0.13 ± 0.03 RHG; $P = 0.004$) or all combined (0.12 ± 0.04 RHG; $P = 0.004$) *P. totara* seedlings growing under the unmodified forest canopy (Fig. 11A). Unbrowsed seedlings under large gaps grew at 200% the rate of unbrowsed seedlings under small gaps. However, animal browse within large gaps limited mean seedling height (0.38 ± 0.08 RHG) to an extent that there was no significant difference (all $P > 0.05$) in mean height growth performance between large gaps and any other gap treatment (Fig. 11A). Under small gaps, all combined (0.31 ± 0.06 RHG) and unbrowsed (0.24 ± 0.06 RHG) *P. totara* seedlings achieved greater mean height growth compared to those under unmodified forest canopy, although those height growth differences were not statistically different ($P > 0.05$). Nor was *P. totara* growth significantly different (all $P > 0.05$) for any other gap treatment–browse status combination (Fig. 11A).

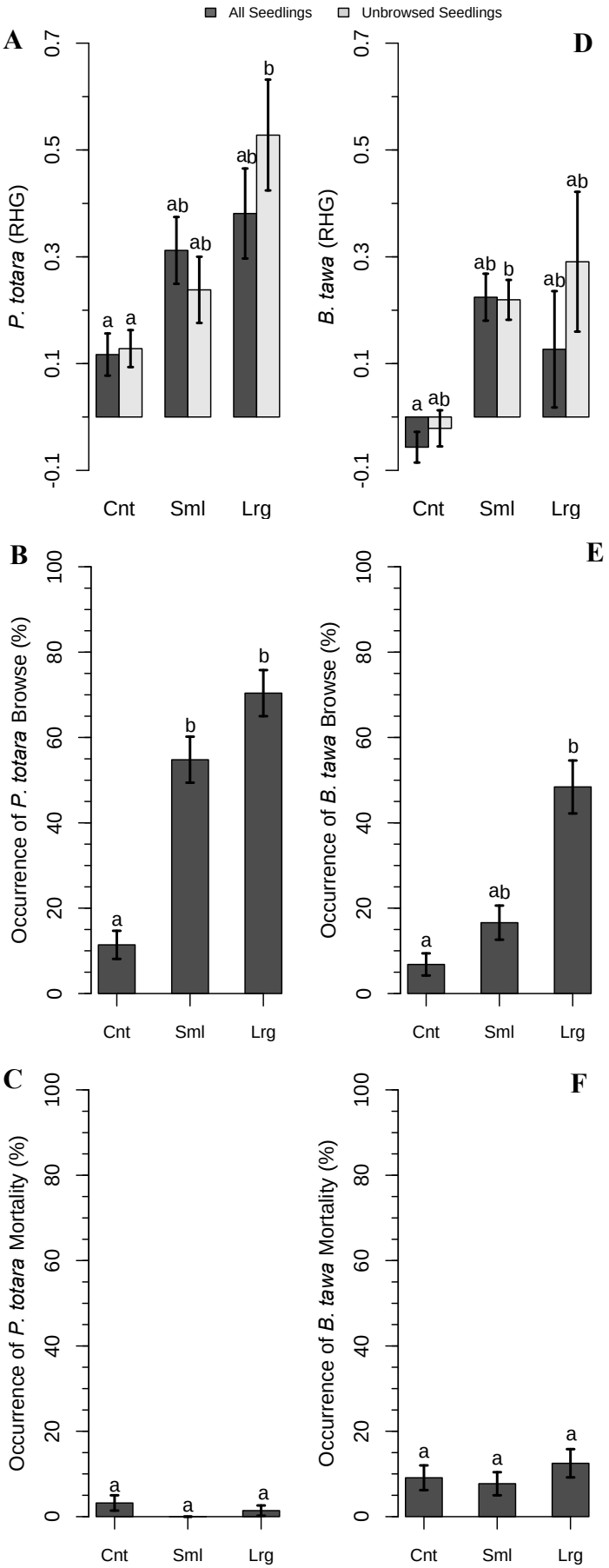


Figure 10. Seedling performance 17 months following experimental canopy gap creation within 18-year-old *Pinus radiata* plantation forest, Marlborough Sounds, South Island, New Zealand.

Experimental treatments were intact forest canopy (Cnt), small gap (Sml), and large gap (Lrg). Note RHG rates (A & D) are given separately for seedlings unaffected by mammalian browse ("Unbrowsed Seedlings") and browsed and unbrowsed seedlings combined ("All Seedlings"). Columns with coinciding letters indicate no significant difference, whereas columns with different letters indicate significant differences at $P < 0.05$. Error bars represent ±1 SE.

The proportion of *P. totara* seedlings affected by animal browse differed significantly among the gap treatments (Generalised Linear Regression, $F(2,18) = 8.099$, $P = 0.003$) (Fig. 11B). *Podocarpus totara* seedlings growing under either small ($54.8 \pm 5.4\%$; $\beta = 2.199$, $P = 0.017$) or large ($70.4 \pm 5.4\%$; $\beta = 2.876$, $P = 0.002$) gaps received a significantly greater occurrence of animal browse compared to those *P. totara* seedlings growing under unmodified canopy ($11.4 \pm 3.3\%$). The difference in occurrence of animal browse of *P. totara* seedlings between small and large gaps was not significant ($\beta = 0.676$, $P = 0.601$).

Gap size and occurrence of animal browse explained a significant amount of the variance in the height growth of *P. totara* seedlings (Multiple Linear Regression, $F(5,15) = 10.45$, $P = < 0.001$, $R^2 = 0.78$, $R^2_{\text{Adjusted}} = 0.70$) (Table 6). Gap creation and *P. totara* height growth were positively associated, and the occurrence of animal browse was negatively associated, with *P. totara* height growth. Both small and large gap treatments significantly predicted *P. totara* seedlings height growth. The occurrence of animal browse was not a significant predictor of *P. totara* height growth. A significant interaction ($\beta = 23.769$, $P = 0.028$) occurred for *P. totara* height growth between animal browse in small gap treatments, meaning height growth in small gaps is likely to be dependent on the extent of animal browse.

Table 6. Multiple regression model fitted to estimate the effect of canopy gap size and the occurrence of mammalian browse on the height growth of indigenous *Podocarpus totara* seedlings planted within two sizes of experimental canopy gaps created with 18-year-old exotic *Pinus radiata* plantation, Marlborough Sounds, New Zealand.

Podocarpus totara

	Estimate	SE	*t*	*P*
(Intercept)	2.75	20.87	0.13	0.897
Small gap	71.22	23.52	3.03	0.008 **
Large gap	140.35	25.25	5.56	< 0.001 ***
Browse occurrence	-12.51	8.34	-1.52	0.150
Small gap: Browse occurrence	23.77	9.75	2.44	0.028 *
Large gap: Browse occurrence	-9.51	9.86	-0.97	0.350

Gap size explained a significant amount of the variance in the height growth of unbrowsed *P. totara* seedlings (Simple Linear Regression, $F(2,13) = 12.4$, $P = < 0.001$, $R^2 = 0.66$). A positive association was found between gap creation and *P. totara* height growth. Gap size significantly predicted unbrowsed *P. totara* seedling height growth for large gaps ($\beta = 111.46$, $P = < 0.001$), but not for small gaps ($\beta = 36.87$, $P = 0.073$).

Podocarpus totara seedling mortality did not differ significantly among gap treatments (all $P > 0.05$) (Fig. 11C), with mortality rates of 3.2% (± 2.0) under unmodified canopy, 0% under small gaps, and 1.4% (± 1.2) under large canopy gaps.

Beilschmiedia tawa

Initial mean absolute *B. tawa* height was 228 mm (± 4), and these seedling heights were not significantly different among experimental plots (one-way ANOVA, $F(2,19) = 2.68$, $P = 0.094$). Seventeen months after gap creation, mean height growth of *B. tawa* seedlings differed significantly among gap treatments (Kruskal-Wallis rank-sum, $H(5) = 17.782$, $P = 0.003$) (Fig. 11D). Mean absolute seedling heights by

treatment were: “control unbrowsed” = 227.5 mm (± 10); “control all combined” = 220.5 mm (± 10); “small unbrowsed” = 267.6 mm (± 15); “small all combined” = 268.1 mm (± 16); “large unbrowsed” = 293.5 mm (± 27); “large all combined” = 217.1 mm (± 43). The significant difference ($P = 0.041$) in *B. tawa* height growth was between all combined seedlings under unmodified canopy (-0.06 ± 0.03 RHG) and unbrowsed *B. tawa* under small gaps (0.23 ± 0.04 RHG). Under large gaps, all combined (0.13 ± 0.11 RHG) and unbrowsed (0.29 ± 0.13 RHG) *B. tawa* seedlings showed considerable variability in height growth. *Beilschmiedia tawa* height growth was most consistent under small gaps and was, on average, negative under unmodified forest canopy.

The proportion of *B. tawa* seedlings affected by animal browse differed significantly among gap treatments (Generalised Linear Regression, $F(2,18) = 4.831$, $P = 0.021$) (Fig. 11E). *Beilschmiedia tawa* browse was significantly ($\beta = 2.552$, $P = 0.024$) greater under large gaps (48.4 ± 6.2%) compared to unmodified forest canopy (6.8 ± 2.6%). Differences in the occurrence of animal browse to *B. tawa* seedlings between small and control ($\beta = 1.006$, $P = 0.591$), and small and large ($\beta = 1.547$, $P = 0.115$) canopy gap treatments were not significant.

Gap size and occurrence of animal browse explained a significant amount of the variance in the height growth of *B. tawa* seedlings (Multiple Linear Regression, $F(3,17) = 11.18$, $P = 0.002$, $R^2 = 0.66$, $R^2_{\text{Adjusted}} = 0.60$) (Table 7). All canopy treatments were significant predictors of *B. tawa* height growth, as was the occurrence of animal browse (all $P < 0.001$). Height growth of *B. tawa* was positively associated with canopy gap creation and negatively associated with both intact forest canopy and the occurrence of animal browse. For *B. tawa* height growth, there was no significant interaction ($P > 0.05$) between gap size and the occurrence of animal browse.

Table 7. Multiple regression model fitted to estimate the effect of canopy gap size and the occurrence of mammalian animal browse on the height growth of indigenous *Beilschmiedia tawa* seedlings planted within two sizes of experimental canopy gaps created with 18-year-old exotic *Pinus radiata* plantation, Marlborough Sounds, New Zealand.

Beilschmiedia tawa				
	Estimate	SE	*t*	*P*
(Intercept)	-66.81	16.38	-4.08	< 0.001 ***
Small gap	81.09	16.91	4.79	< 0.001 ***
Large Gap	99.31	21.98	4.52	< 0.001 ***
Browse occurrence	-17.34	4.25	-4.07	< 0.001 ***

Gap size explained a significant amount of the variance in the height growth of unbrowsed *B. tawa* seedlings (Simple Linear Regression, $F(2,16) = 8.96$, $P = 0.002$, $R^2 = 0.53$). Both small ($\beta = 59.16$, $P = 0.004$) and large ($\beta = 74.75$, $P = 0.002$) gap sizes significantly predicted *B. tawa* height growth.

The occurrence of *B. tawa* seedling mortality did not differ significantly (Generalised Linear Regression, $F(2,18) = 0.226$, $P = 0.799$) among gap treatments (Fig. 11F), with *B. tawa* mortality rates of 9.1% (± 2.9) under unmodified canopy, 7.7% (±2.7) under small gaps, and 12.5% (± 3.3) under large canopy gaps.

4.5. DISCUSSION

4.5.1. Small-scale Canopy Gaps Optimise Understorey Light Environment

Canopy interventions within even-aged exotic plantation monocultures provide a means of diversifying forest structure and composition, thereby improving forest habitat and associated biological diversity (Lindenmayer et al., 2006; Coates & Burton, 1997), and creating conditions that would otherwise take an extended period of time to develop naturally (Kuuluvainen et al., 2002). As predicted, we found that

small-scale canopy gap formation in an 18-year-old exotic *P. radiata* plantation significantly increased light transmission to the forest understorey and increased height growth rates of planted indigenous *P. totara* and *B. tawa* seedlings. We also found that species with differing requirements for light performed differently according to canopy gap size. Light-demanding *P. totara* showed an increased rate of height growth in large gaps, while *B. tawa* height growth increased with gaps of any size, although *B. tawa* growth was less variable under small gaps.

These results are consistent with the existing literature, which shows that artificial canopy gap size plays a significant role in controlling light transmission to the forest understorey, and also that artificial gaps within plantation forests can be sized to provide optimum light conditions for the recruitment of specific forest tree species in restoration. Within a *P. thunbergii* plantation, in coastal Japan, > 1-year-old seedlings increased in density and growth with increasing size of artificial canopy gap, or canopy openness (Zhu et al., 2003). A minimum gap size for the survival of *P. thunbergii* seedlings was determined to be ≥ 1.0 gap ratio, or > 30% canopy openness. Gaps of ≥ 1.5 gap ratio, or > 40% canopy openness, were required for *P. thunbergii* seedlings to achieve sapling growth stage.

In contrast, our data for New Zealand temperate forest tree seedlings within an 18-year-old *P. radiata* plantation show a lower requirement for light. In our central New Zealand study area, we found that gap ratio and canopy openness values of 0.40 gap ratio/18.2% and 0.58 gap ratio/25.6% were best for growth of *B. tawa* and *P. totara*, respectively. We would expect some variability in seedling growth performance among plantations of different physical attributes or geographical location and these are aspects we have not be able to assess in our experiment as it was carried out in a single plantation.

In Ontario, Canada, thinning treatments within a *Pinus resinosa* plantation created canopy openness and percentage light transmission within the ranges 15–29% and 13.3–33.5%, respectively. Five years after thinning, indigenous seedling diameter, height, and stem volume were positively correlated with both thinning intensity and canopy opening size (Parker et al., 2001). Seedling stem relative growth rates of *Fraxinus*, *Pinus*, and *Quercus* differed significantly among different sized

canopy openings (Parker et al., 2001). In Sri Lanka, tropical forest canopy tree species were successfully established under artificial canopy openings within a *P. caribaea* plantation forest. In this study, satisfactory seedling establishment required gap sizes that transmitted at least 50% of total available light, and 4-5 times the amount of light available under intact *P. caribaea* canopy (Ashton et al., 1997), a considerably greater light requirement than created in our *P. radiata* gap treatments.

Our results are consistent with existing knowledge regarding the light requirements of *P. totara* and *B. tawa* (Lusk et al., 2009; Smale et al., 2008; Ebbett & Ogden, 1998; Smale & Kimberley, 1986). Total solar radiation under the unmodified forest canopy (0.44 mol m^{-2} d^{-1}) was similar to the light compensation point reported by Lusk et al. (2015) for *P. totara* (0.42 mol m^{-2} d^{-1}) and considerably greater than the light compensation points reported for *B. tawa* of 0.08 mol m^{-2} d^{-1} (Lusk & Jorgensen, 2013) and 0.09 mol m^{-2} d^{-1} (Lusk et al., 2015). Our mean per-annum scaled growth rate for unbrowsed *P. totara* (22 mm $year^{-1}$) under the intact *Pinus* canopy is intermediate between those growth rates found under approximately equivalent illuminations by Ebbett and Ogden (1998) from a glasshouse trial (572 mm $year^{-1}$ (± 146 SD) at 25% of full sunlight) and from mature open *W. racemosa* forest with *Kunzea ericoides* (Myrtaceae) and *B. tawa* (24 mm $year^{-1}$ (± 15 SD) at 20% of full sunlight), within the Whirinaki Forest Sanctuary, central North Island (Ebbett & Ogden, 1998). In contrast, *B. tawa* seedling growth rates are intrinsically slow and, in some circumstances, may be negative (West, 1995) or variable (Knowles & Beveridge, 1982). Under the intact *Pinus* canopy in the current study, due to a combination of slow-growth rate and apical die-back, unbrowsed *B. tawa* growth rates were negative (-8 mm $year^{-1}$), and in large gaps growth was highly variable, although the high degree of exposure in large gaps might explain this variability. Unbrowsed *Beilschmiedia tawa* growth rates from small gaps (34 mm $year^{-1}$) and large gaps (45 mm $year^{-1}$) are less than the 50–300 mm $year^{-1}$ range found by Knowles and Beveridge (1982) in their releasing trial within indigenous shrub hardwood cover.

4.5.2. Implications of Animal Browse

Gap creation was associated with an increase in the occurrence of animal browse. The foliage of *B. tawa* and *P. totara* are both moderately palatable to

Trichosurus vulpecula (Sweetapple et al., 2013). While both *B. tawa* and *P. totara* are recognised as generally being avoided in the diet of introduced ungulates, ungulate browse of these species does occur (Forsyth et al., 2003) and young *P. totara* shoots can be a preferred food for deer at times when foliage nutrient levels are seasonally elevated. While there is evidence from European temperate forests (Kuijper et al., 2009) that ungulates, and in particular *Cervus elaphus scoticus*, preferentially forage within forest clearings, we are unable to say from our data whether it was the gap per se, or the additional planted seedling and exotic herbaceous plant growth occurring within the higher light environments of gaps, that caused the increased browse occurrence. *Podocarpus totara* height growth increased in large gaps only for unbrowsed seedlings. When browsed *P. totara* seedlings were taken into account, there were no significant differences in height growth among gap treatments, and the apparent benefit of gap creation was reduced. In large gaps, where *B. tawa* browse was greatest, animal browse significantly limited *B. tawa* seedling height growth.

4.5.3. Exotic *Pinus* Gaps for Forest Restoration

In the New Zealand context, our results suggest that, if *P. totara* seedlings can be protected from animal browse, then large canopy gaps (e.g., gaps typically of 5.6 m radius; 0.58 gap ratio; 84% of total available light transmitted) in mid-rotation *P. radiata* plantation stands would be preferable to smaller gaps, or intact forest canopy, for establishing this species. The benefit of large gaps to unbrowsed *B. tawa* seedling height growth is uncertain. Considering the high variability in *B. tawa* height growth data from large gaps, along with the species' known strong shade-tolerance and sensitivity to exposure (Knowles & Beveridge, 1982), small gaps (e.g., gaps typically of 2.3 m radius; 0.40 gap ratio; 50% of total available light transmitted) are likely to be optimal over either intact forest canopy or large gaps, for *B. tawa* recruitment. While not assessed in our experiment, we do note that light gradients differ across forest gaps (e.g., shaded gap edge vs. highly illuminated gap centre). We suggest that with some further assessment, it may be possible to incorporate a diversity of species with differing shade tolerance into artificial canopy gaps, by locating species in suitable gap microsites according to species-specific shade tolerance and gap light distribution.

Given the increased occurrence of animal browse from gap creation, in circumstances where animal browse cannot be prevented, our results suggest that, for *P. totara*, large canopy gaps are likely to be preferable to small canopy gaps. However, high-density plantings may be required to mitigate against the effects of animal browse. For *B. tawa*, our results provide evidence that animal browse under small gaps had little effect on seedling height growth. These results mean smaller gaps are likely to be the best for *B. tawa* seedling growth, regardless of the degree of animal browse.

Internationally, plantations are recognised for the role they play in increasing landscape connectivity, buffering existing forest remnants, providing habitat for both common and threatened species, and conserving soil and water resources (Brockerhoff et al., 2008; Carnus et al., 2006). Global trends of increasing cover by plantation forest (Food and Agriculture Organisation of the United Nations [FAO], 2011) coupled with the role of habitat change on global declining biodiversity trends (Pereira et al., 2012) suggest opportunities for biodiversity management can be found in improved plantation management.

From their outset, plantations may be managed for non-harvest purposes, such as soil or water conservation, or changes in social or cultural values over their lifetime may mean they are not intended to be harvested. Under these circumstances, non-harvest plantations provide one approach for restoring indigenous forest communities, and provide a means of managing plantations to maximise indigenous species success. As our gap experiment was conducted in only one plantation we are unable to assess the effects of variables that affect seedling performance in gaps of given dimensions, and that might vary among plantations. Such factors include *Pinus* age class, slope aspect, geographical location, and soil type. Therefore, there is scope for further gap experiments in *P. radiata* plantations of different age classes and on different topographies and soils, and also with different indigenous species – taking into account species-specific shade tolerance and palatability. Nevertheless, our results provide further support to the existing literature that shows canopy gap interventions are a means of promoting indigenous forest recruitment from plantation understories, and this intervention is likely to assist in achieving multiple non-harvest forest restoration management objectives.

5. CHAPTER FOUR:

Tree Fern Competition Reduces Indigenous Forest Tree Seedling Growth within Exotic *Pinus radiata* Plantations

CHAPTER PREFACE

Chapter Two identified the constraints imposed on forest regeneration by the competitive shading of dense understorey vegetation. Adult tree ferns were observed entering the chronosequence at 15–25 years, and continued to increase in dominance with increasing stand age. The recognised effect of tree ferns in casting deep shade in New Zealand's natural forest was noted, and it was highlighted that where *P. radiata* plantations have tree fern dominated understories, this might present a significant limitation on the ability of mature forest canopy species to regenerate.

Chapter Three established that creating small-scale canopy gaps in even-aged *P. radiata* plantation canopy is a means of increased light levels in the forest understory, which led to significant outcomes for the performance of planted seedlings of mature forest canopy species.

Chapter Four builds on these previous chapters, through an investigation into the competitive effect of tree fern dominance on growth rates of two mature forest canopy species planted within mature *P. radiata* plantations. In a similar vein to the canopy gap experiment, which aimed to address the competitive shading effects of the homogenous plantation canopy on woody seedling growth, Chapter Four addresses the competitive shading effect of dense understorey vegetation, which is particularly relevant to central North Island *P. radiata* plantations, where tree ferns commonly dominate mature *P. radiata* plantation understories.

Chapter Four has been published in the journal Forest Ecology and Management. My Supervisors, Prof. David Norton and Dr. Fiona Carswell, are co-authors of the manuscript. This paper is enclosed as Appendix D, and the citation for the paper is:

Forbes, A. S., Norton, D. A., & Carswell, F. E. (2016). Tree fern competition reduces indigenous forest tree seedling growth within exotic *Pinus radiata* plantations. *Forest Ecology and Management, 359,* 1–10.

The tree fern composition across the 30 experimental plots was described and published as supplementary information, and that information is enclosed as Appendix E.

5.1. ABSTRACT

Tree ferns are recognized as "keystone" species for their role in casting deep shade on forest floor environments, acting as a differential ecological filter on forest regeneration processes. Tree fern dominance is a feature of New Zealand's central North Island exotic *Pinus radiata* (Pinaceae) plantations, particularly beyond 20 years following plantation establishment. In circumstances where plantation forests are managed for restoration of indigenous forest species, rather than timber harvest, an understanding of the competitive role of dense tree fern stands on forest regeneration processes in these "non-harvest" plantations is necessary.

We investigated the competitive effect of tree fern (Cyatheaceae and Dicksoniaceae) cover on seedling growth rates of two mature forest tree species, *Podocarpus totara* (Podocarpaceae) and *Pittosporum eugenioides* (Pittosporaceae), over two austral summers in five 36–92-year *P. radiata* plantations. We experimentally manipulated tree fern canopies in order to contrast heavy versus light shading. Tree fern removal significantly increased the growth rate of both *P. totara* and *P. eugenioides*, and the growth rate of the shorter-lived, faster-growing, light-demanding *P. eugenioides* was greater than that of *P. totara* with tree fern removal. Damage to the seedlings by mammalian animal browsers when tree ferns were removed was greater than that occurring under tree fern cover. This damage diminished the effect of tree fern removal on seedling growth rates for *P. totara*, but not for the faster growing *P. eugenioides*.

The physical clearance of tree fern stands and then the establishment of fast growing, locally representative, indigenous canopy tree species of low palatability, along with protection from animal browse, are suggested restoration strategies. Our results are consistent with existing literature in showing that where tree ferns are a dominant feature of plantation understories, deep shade is likely to reduce canopy species seedling growth rates, reducing the potential for forest regeneration.

5.2. INTRODUCTION

The interception of light by dense understorey vegetation can have a profound effect on forest regeneration processes, and ultimately the rate and trajectory of forest successions (Royo & Carson, 2006; George & Bazzaz, 1999; Bazzaz & Pickett, 1980). Steep gradients of declining photosynthetically active radiation near the forest floor shape the structure and composition of the seedling bank, which directly influences the competitive and reproductive dynamics of forest regeneration (George & Bazzaz, 1999). Through competitive processes, tree fern dominated forest understories have been found to exert an ecological filtering effect ("fern filtering") on tree regeneration processes (Bystriakova et al., 2011; Coomes et al., 2005). In particular, given the deep shade cast by tree ferns' near horizontally-arched megaphyll fronds, tree ferns are increasingly recognized as "keystone species" (cf. Paine, 1969) due to their disproportionally large influence on forest floor regeneration processes (Gaxiola et al., 2008; Coomes et al., 2005; Newton & Healey, 1989).

As a result of their prolific spore production, tree ferns have the ability to rapidly colonise disturbed areas (Conant, 1976), and in some species such as *Dicksonia squarrosa* (Dicksoniaceae) also through clonal growth (spreading rhizomes). Following volcanic disturbance on recent substrates of the Hawaiian Islands, tree ferns (*Cibotium* spp.) often vigorously invade the nutrient-enriched soils, forming a dense canopy cover and casting heavy shade (Mueller-Dombois, 2000; Drake & Mueller-Dombois, 1993). Tree ferns of the genus *Cyathea* also form dense stands on landslide substrates in Puerto Rico, arresting woody successions for decades (Walker et al., 2010). In New Zealand's indigenous, temperate, podocarp-broadleaved forest, tall tree ferns intercept about half of the incoming radiation and reduce the ability of conifers to escape the competitive effects of the faster growing angiosperms (Coomes et al., 2005). In a similar vein, Carswell et al. (2007) found that conifers (Podocarpaceae) were not likely to occur in areas with high amounts of tree fern cover, and Gaxiola et al. (2008) manipulated tree fern stands, finding that frond removal significantly increased the height growth rate of seedlings (podocarp and angiosperm) planted on the forest floor.

Tree fern dominated understories also potentially develop within plantation forests (Harrington & Ewel, 1997; Ogden et al., 1997; Allen et al., 1995). While in commercial plantations held under a clear-fell harvest regime the extent of indigenous regeneration within the forest understorey can be limited, in some situations plantation owners want to retain their plantation to provide a nurse environment for the restoration of indigenous forest species (Carnus et al., 2006; Lamb et al., 2005; Lamb, 1998; Parrotta, 1992). In these situations, the highly competitive understorey layers that are formed by tree ferns can limit the establishment of woody species (Nuttle et al., 2014; De la Cretaz & Kelty, 2002). Therefore, when tree fern dominated understories develop within these "non-harvest" plantations, forest and restoration managers require an understanding of the competitive role tree ferns have in the plantations' regeneration dynamics and how this might be manipulated to accelerate forest regeneration.

As of 2014, it was estimated that 7% (1.75 million ha) of New Zealand's land cover was occupied by plantation forests, the majority being located in the North Island (1.23 million ha), with a particular concentration of plantation forest in the central North Island (587,104 ha) (Ministry of Primary Industries [MPI], 2014). Ninety percent of New Zealand's plantation cover comprises *Pinus radiata*, with the remaining area comprising Douglas-fir (6%), Eucalypt (1%), and other softwood and hardwood species (3%) (MPI, 2014). Over the first two decades following plantation establishment, the understories of central North Island exotic *P. radiata* plantations often become colonised by tree fern species (Cyatheaceae and Dicksoniaceae), which increase in dominance over subsequent decades (Ogden et al., 1997). In plantation forests close to our study area, *P. radiata* stands > 30-years-old achieved a total basal area comprising 10–30% tree ferns and tree fern stem densities totaled 2000–2500 stems ha^{-1} (Ogden et al., 1997). Cyatheaceae and Dicksoniaceae tree fern species differ in their life history traits regarding growth rate and shade tolerance (Bystriakova et al., 2011). Within central North Island *P. radiata* plantations, the relative abundance among tree fern species changes as understorey illumination is altered over time by stand development (Ogden et al., 1997). Following plantation establishment, *Dicksonia* species appear during the first decade, whereas *Cyathea* species are gradually added during the second decade, and become more abundant with time. *Dicksonia squarrosa*, which is New Zealand's most common tree fern

(Bystriakova et al., 2011), is known to dominate the tree fern community (Ogden et al., 1997). It is the only New Zealand tree fern species to reproduce via aerial buds (Large & Braggins, 2004), thereby taking on a multi-stemmed form and is also rhizomatous; forming potentially large, interconnected colonial stands (Brownsey & Smith-Dodsworth, 2000).

As the restoration potential of plantations is likely to be limited when the recruitment of future canopy tree species on the site is constrained by very dense understories (Nuttle et al., 2014; Royo & Carson, 2006; De la Cretaz & Kelty, 2002), we suggest dense stands of tree fern cover (Fig. 12) may limit recruitment of indigenous canopy tree species within these central North Island exotic *P. radiata* forests, thereby limiting their potential biodiversity value.

Figure 11. Example of tree fern dominated forest understorey composition within mature *Pinus radiata* plantation forest, central North Island, New Zealand.

Here, we examine the shading effect of dense tree fern stands on the growth of seedlings of two indigenous forest canopy species, *Podocarpus totara* (Podocarpaceae) and *Pittosporum eugenioides* (Pittosporaceae), planted within exotic *P. radiata* plantations. We have experimentally manipulated the tree fern canopy in order to contrast heavy versus light shading of seedlings by tree ferns. We predict that the heavy shade cast by tree ferns will reduce the growth rate of these two indigenous forest canopy species, and we expect the species' contrasting life history traits to provide insights into the effect of heavy tree fern shade on an indigenous forest succession from exotic *P. radiata* plantations in New Zealand. *Podocarpus totara* is a long-lived (800–900 years; Hinds & Reid, 1957), albeit relatively light-demanding conifer (Ebbett & Ogden, 1998), which is generally avoided in the diet of introduced ungulates. However, ungulate browse does occur (Forsyth et al., 2002), and young *P. totara* shoots can be preferentially browsed when nutrient concentrations are seasonally elevated. *Pittosporum eugenioides* is a shorter lived angiosperm that exhibits faster growth rates (Williams & Buxton, 1989), is generally avoided in the diet of introduced ungulates (Forsyth et al., 2002), and is a species usually found in the early stages of New Zealand's indigenous forest successions. Therefore, we predict that under the heavy shade cast by tree fern stands under the *P. radiata* canopy—the longer-lived conifer *P. totara* will be less competitive than the faster-growing, more light-demanding angiosperm *P. eugenioides*.

5.3. METHODS

5.3.1. Study Area

The study was undertaken in Kaingaroa Forest, northern Kaingaroa Plateau, central North Island, New Zealand (38°23'44"S 176°30'11"E, 375–510 m), a large (180,000 ha) commercial exotic plantation forest. The plateau landform comprises volcanic ignimbrite rock layers that have resisted erosion (Vucetich et al., 1960), although some topographical variation from fluvial down cutting occurs at the plateau margins. Soils are Orthic Allophanic or Orthic Pumice (Landcare Research [LCR], 2015) (Table 8).

Table 8. Characteristics of experimental *Pinus radiata* stands. Tree statistics relate to *P. radiata* only

Stand ref.	Age (yrs.)	Area (ha)	Canopy ht.[a] (m)		Stem dia. (cm)		Stem freq. (stem ha^{-1})	Basal area (m^{-2} ha^{-1})	Elev. (m)	Rotation	Soil
			M±SEM	*n*	*M*±SEM	*n*	*M*±SEM	*M*±SEM			
A	36	2.03	41.5±1	*7*	50.0±2	*57*	237.5±29	49.9±5	440–510	2	Acidic Orthic Allophanic
B	48	13.81	32.2±1	*0*	51.6±3	*70*	259.3±42	65.2±11	375–425	2	Buried-Allophanic Orthic Pumice
C	67	0.60	37.1±1	*9*	55.4±3	*39*	325.0±34	84.1±13	450–475	1	Immature Orthic Pumice
D	72	3.75	51.6±2	*3*	80.6±3	*23*	153.3±17	79.9±13	395–420	1	Immature Orthic Pumice
E	92	2.90	39.1±3	*2*	54.3±5	*55*	203.7±41	71.2±17	480–510	1	Immature Orthic Pumice

Notes. Stem freq. = stem frequency; Stem dia. = stem diameter; Elev. = elevation in metres above mean sea level. Rotation = the total number of plantation cycles at the site; *M* = sample mean; SEM = one standard error of the mean; *n* = sample size, refers to the number of trees measured for Canopy ht. and Stem dia.; and the number of plots measured for Stem freq. & Basal area. [a]For stand ref. E, regenerating *P. radiata* trees of < 20 m tall were removed from this mean tree height calculation as those trees did not represent forest canopy height.

The climate is relatively wet, with a mean (1914–1999 mean) annual rainfall of 1480 mm (National Institute of Water and Atmospheric Research [NIWA], 2013). Daily mean air temperatures range from 16°C in January to 5°C in July, and the annual mean temperature is 11°C. Frosts are a feature of the local climate and may occur anytime between March and December, most often between May and September. Temperatures typically fall to -3°C to -4°C during winter or early spring, and minimum temperatures as low as -9.4°C have been recorded (NIWA, 2013). All climate statistics are taken from the Kaingaroa Village Climate Station.

Prior to human settlement (c. 730 years ago; Wilmshurst et al., 2008), indigenous podocarp-broadleaved forest covered the Kaingaroa Plateau (Leathwick 2001, 2004; Williams & Walton, 2003). Subsequent vulcanism and associated wildfires (Perry et al., 2014; Vucetich et al., 1960), together with vegetation clearance resulting from human settlement (Boyd, 1992), severely reduced the extent of this forest cover.

Significant introduced browsing mammals present within the study area are brushtail possum (*Trichosurus vulpecula*), red deer (*Cervus elaphus scoticus*), sika deer (*Cervus nippon*), and the soil-disturbing feral pig (*Sus scrofa*) (King, 1990).

5.3.2. Experimental Design

We selected five *P. radiata* plantation stands ranging in age from 36–92 years (at 2013), located within an 18.5 km area of the wider (180,000 ha) plantation forest. The structural characteristics of the five experimental *P. radiata* plantation stands are presented in Table 8. These stands were selected as they are older than the typical commercial rotation age (25–30 years) and are non-harvest stands with some forest restoration potential and the forest owners intend to retain them in an unharvested state within the plantation matrix (C. Maunder 2013, Timberlands Limited, personal communication).

Experimental treatment types related to the status of tree fern cover. Treatments were either: tree fern cover intact (TF), tree fern cover removed (TFR), or no tree fern cover (NTF, control). The treatments TFR and NTF represented sites with little to no effective shading from tree fern foliage. The TFR treatment plots were created by felling all tree ferns within 2.3 m (16 m^2) of the randomly located plot center. The TF treatment represented sites amongst tree fern stands that were exposed to the shade cast by tree fern fronds. Three plots

of each treatment type (i.e., TF, TFR, NTF) were distributed within each of the five plantation stands. Randomly generated plot coordinates were assigned to experimental treatment types at random, which were then located in the field using a handheld global positioning unit (Garmin 62s). In locations that were assigned to an NTF treatment but had tree ferns present, the nearest tree-fern free area was selected as the NTF plot location. To prevent edge effects, random plot locations were excluded from a 20 m buffer around the plantation edge. Interference between plots was avoided by the imposition of a minimum 15 m separation between plots.

Tree fern stands were predominantly composed of *Dicksonia squarrosa*. *Dicksonia fibrosa* (Dicksoniaceae), *Cyathea medullaris*, *C. dealbata*, and *C. smithii* (Cyatheaceae) also occurred within experimental treatments. To restrict shading influence to only the *P. radiata* and tree fern canopies, any other plants with the potential to cast shade were removed from the vicinity of plots.

5.3.3. Field Survey

We used the Mesoscale Topographic Index (McNab, 1993) to assess any differences in site exposure among plots. This comprised the mean of eight equidistant slope to horizon measurements from each plot center. Hemispherical photography was used to quantify both forest percentage canopy openness and transmitted photosynthetically active radiation (PAR; mol m^{-2} d^{-1}) at all plots. Percentage canopy openness represents the percentage of open sky seen from beneath a forest canopy and total transmitted PAR represents the sum of direct and indirect PAR transmitted by the forest canopy (Frazer et al., 1999).

Hemispherical canopy photography was repeated at TFR plots after tree fern thinning to quantify the effect of tree fern thinning on canopy openness and light transmission. One hemispherical photograph was taken at 1.35 m height above ground at the center of each plot, using a Pentax K200 DSLR fitted with a Sigma 4.5 mm circular hemispherical (fisheye) lens. *Pinus radiata* plantation stand structure was quantified by the measurement of tree height and diameter within a 0.03 ha circular plot measured around each experimental plot center. The diameter at breast height (dbh) was measured at 1.35 m. Occasionally, the 0.03 ha *P. radiata* canopy tree plots would overlap and, in those instances, only one of the two *P. radiata* canopy tree plots was measured in order to maintain independence among the canopy tree

samples. This resulted in a slightly reduced *P. radiata* sample size for calculation of *P. radiata* statistics at several plantations, but presented no limitations to the study.

Tree fern measurements were based on a basal area prism sweep (Bitterlich, 1984) from each experimental plot center. All tree ferns within a prism sweep (Factor 4) were identified to species level, tallied, and their height and dbh measured. Tree fern height was measured from ground level to the base of the lowest live frond. Tree fern basal area was determined for each plot by multiplying the prism-derived stem count by four (the prism factor). To quantify the effect of tree fern thinning on tree fern stand structure, basal area sweeps were repeated at TFR plots following tree fern thinning. As a basal area sweep might have detected tree ferns located at a distance beyond where they would cast shade over the planted seedlings, the sweep-derived data provided a relative measure of tree fern stand structure among treatments, rather than a direct measure of the degree of shade cast over the experimental plot. Instead, a direct measure of canopy openness and light transmission was provided by the hemispherical photography survey.

Locally sourced nursery raised potted seedlings of *P. totara* and *P. eugenioides* (nine seedlings of each species per plot) were planted in an alternating grid arrangement, with the planted grid centered on the plot center point. Seedlings were planted at 50 cm spacing resulting in a planted area of 4 m^2 around the center where light transmission and canopy openness was measured from. Initial seedling heights were measured during August 2013, with repeat seedling height measurements occurring 9 (May 2014) and 18 (February 2015) months later, with the last measurement including two austral summers of plant growth.

5.3.4. Statistical Analysis

All statistical analyses were undertaken using R (R Development Core Team Team [R], 2014). Differences in plot aspect among experimental treatments were assessed using functions of the R Circular package (Agostinelli & Lund, 2013), with probability values calculated using the Wallraff rank-sum test of angular distance. Percentage canopy openness data were Logit transformed prior to hypothesis testing using the Wilcoxon rank-sum test. Proportional changes in light transmission were assessed using a Generalised Linear Model (GLM), applying the Binomial family and the default Logit link function. Where GLMs found significant differences (at alpha = 0.05), post-hoc pairwise comparisons of significance

were carried out using the glht function of the R multcomp package (Hothorn et al., 2008), using the default single-step method to adjust *P*-values for multiple comparisons.

Differences in mean values relating to manipulated tree fern stand structure, initial seedling heights, and levels of transmitted PAR among experimental treatments were assessed using either one-way ANOVA or Kruskal-Wallis rank-sum tests. ANOVA and linear regression models were tested for linearity, normality of the residuals, and homoscedasticity with diagnostic plots and through use of the gvlma package (Pena & Slate, 2014) in R. Nonparametric tests were used where model assumptions could not be met through data transformations. Where significant differences were detected (at alpha = 0.05), post-hoc pairwise comparisons were carried out using the Tukey HSD or Nemenyi test, respectively for ANOVA and Kruskal-Wallis tests.

The combined effects of experimental treatments and mammalian animal browse were assessed using Multiple Linear Regression. Percentage explanatory variables were Logit transformed for inclusion in regression modeling. Experimental treatment effects on unbrowsed seedling height growth were assessed using Simple Linear Regression, for which the *P. totara* data required natural log conversion, and both *P. totara* and *P. eugenioides* height growth data from the 18-month experimental period were per-annum scaled.

Differences in the proportional effects of animal browse and seedling mortality were assessed using Generalised Linear Models (GLM), applying the Quasibinomial family with *F*-test when the GLM was overdispersed. Fisher's exact test was used to assess the significance of differences amongst proportional browse or mortality data when a satisfactory GLM could not be specified. All error estimates were one standard error of the mean unless otherwise stated.

Seedling relative height growth (RHG) was calculated using the formula:

$$\mathrm{RHG} = \mathrm{T2} - \mathrm{T1}/\mathrm{T1} \qquad \textit{Equation 1}$$

where T1 and T2 were absolute seedling heights measured in millimeters at the time of experiment establishment and 18 months later, respectively.

Percentage canopy openness and light transmission were extracted from hemispherical photographs using the imaging software Gap Light Analyzer (GLA, Version 2; Frazer et al.,

1999). For GLA modeling, the growing season was defined as 1 September–31 March, the default solar constant used was 1367 Wm^{-2}, and the Cloudiness Index, Spectral Fraction, and Beam Fraction were all set at 0.5.

5.4. RESULTS

5.4.1. Experimental Plot Characteristics

The degree of topographic exposure among experimental treatments was not significantly different, with mean Mesoscale Topographical Index values of 14.4±1% for TF plots, 14.3±1% for TFR, and 13.2±1% for NTF (Kruskal-Wallis rank-sum test, $H(2) = 0.531$, $P = 0.767$). Angular dispersion of plot aspect was not significantly different among treatments (Kruskal-Wallis rank-sum test, $H(2) = 0.084$, $P = 0.959$). Plot aspects were predominantly to east-south-east, with mean aspects of 115±2°SD for TF, 101±1°SD for TFR, and 119±2°SD for NTF. The mean plot slopes of 16.9±2° at TF plots, 20.1±3° at TFR plots, and 15.5±3° at NTF plots were not significantly different (one-way analysis of means, $F2.0,27.7 = 0.823$, $P = 0.450$). There was no significant difference in basal area among treatments in the five *P. radiata* stands (Kruskal-Wallis rank-sum test, $H(2) = 5.257$, $P = 0.072$).

Dicksonia squarrosa had the highest stem densities (1888.3±201 stems ha^{-1}), with lesser densities of *D. fibrosa* (152.0±39 stems ha^{-1}), *C. medullaris* (110±16 stems ha^{-1}), *C. dealbata* (98.6±39 stems ha^{-1}), and *C. smithii* (141 stems ha^{-1}, $n = 1$). Mean tree fern heights did not differ significantly (Kruskal-Wallis rank-sum test, $H(3) = 1.003$, $P = 0.801$) either among treatments, or as a result of tree fern thinning (TF = 3.3±0.2 m, $n = 118$; TFR_{before} = 3.3±0.2 m, $n = 126$; TFR_{after} = 3.1±0.4 m, $n = 25$; NTF = 3.3±0.6 m, $n = 13$).

5.4.2. Experimental Treatment Effects

Tree fern stem density differed significantly among treatments (Kruskal-Wallis rank-sum test, $H(3) = 43.634$, $P < 0.001$; Fig. 13A). Tree fern thinning significantly ($P < 0.001$) reduced mean stem density (TFR_{before} = 1977±328 stems ha^{-1}, TFR_{after} = 311.5±87 stems ha^{-1}). Tree fern stem density in both the TF treatment (2153±260 stems ha^{-1}) and TFR_{after} treatment were significantly greater ($P < 0.001$) than in the NTF treatment (114±55 stems ha^{-1}). No other difference in tree fern stem density among treatments was significant (all $P >$

0.74). Tree fern basal area differed significantly among treatments (Kruskal-Wallis rank-sum test, $H(3) = 40.936$, $P < 0.001$; Fig. 13B).

Tree fern basal area was significantly reduced ($P < 0.001$) by tree fern thinning (TFR_{before} = 33.6±5 m^{-2} ha^{-1}, TFR_{after} = 6.6±1.7 m^{-2} ha^{-1}). Tree fern basal area was significantly less ($P < 0.001$) in the NTF (3.5±1.3 m^{-2} ha^{-1}) and TFR_{after} treatments compared to the TF (31.5±3 m^{-2} ha^{-1}) treatment. All other differences in basal area among tree fern treatments were non-significant (all $P > 0.81$).

Tree fern thinning significantly increased (one-way ANOVA, $F1,28 = 14.23$, $P < 0.001$) both canopy openness (before = 9.9±0.8%, after = 14.3±1%; Fig. 14) and total transmitted PAR (Generalised Linear Model, $X(1) = 18.544$, $P < 0.001$) (before = 14.7±2%, after = 28.0±2%; Fig. 15).

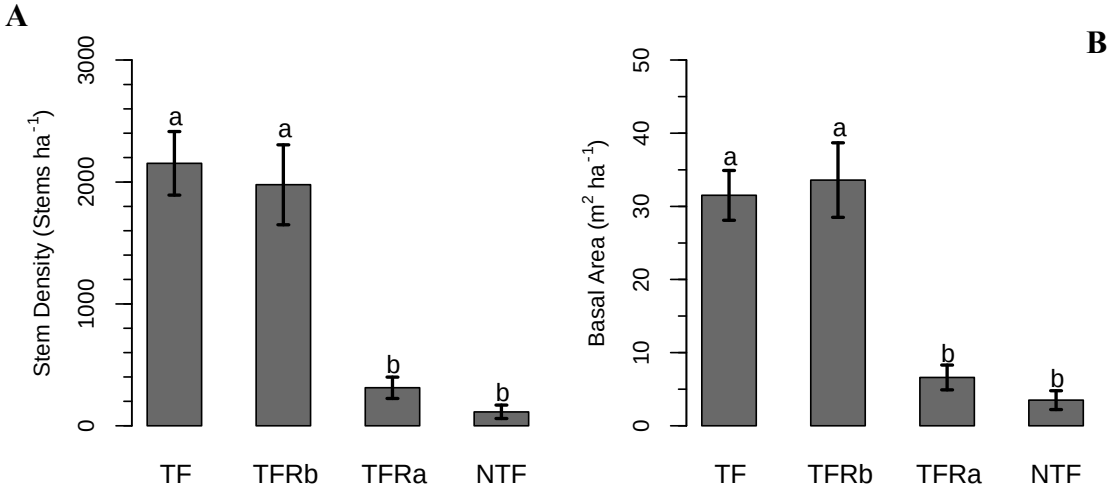


Figure 12. Mean tree fern (A) stem density and (B) basal area according to tree fern status; either tree fern (TF) cover, before (TFRb) or after (TFRa) tree fern thinning, or in areas with no tree ferns (NTF).Experimental stands were five 36–92-year-old *Pinus radiata* plantations, located in Kaingaroa Forest, central North Island, New Zealand. Mean stem density and basal area were calculated from 15 plots in each tree fern status category. Columns with coinciding letters indicate no significant difference, whereas columns with different letters indicate significant differences at $P < 0.05$. Error bars represent ±1SE.

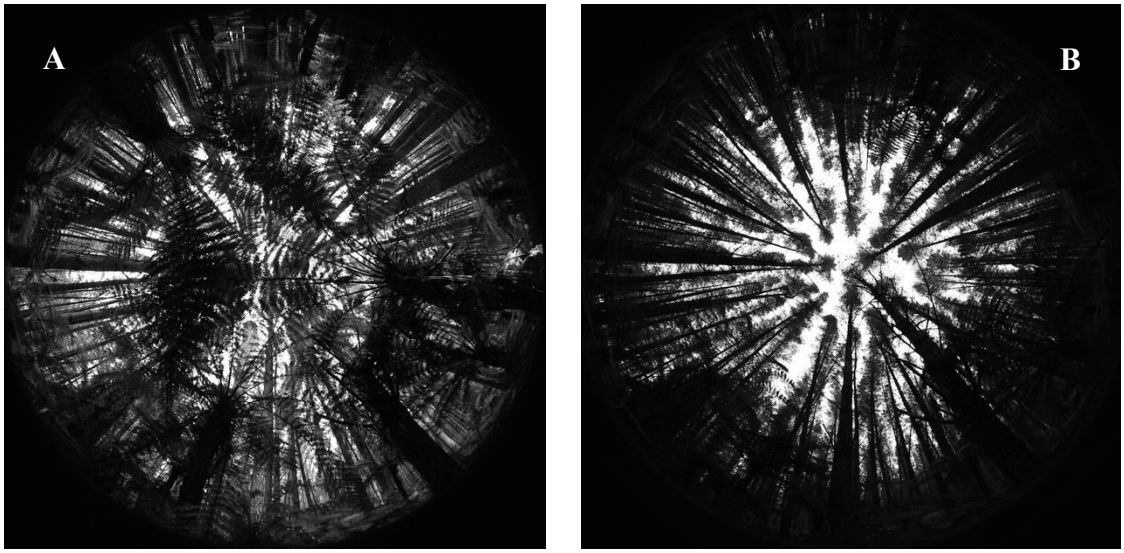


Figure 13. Example of canopy openness (A) before and (B) after tree fern thinning within a commercially mature *Pinus radiata* plantation forest, central North Island, New Zealand. The perspectives presented are 180˚hemispherical (fisheye) photographs taken at 1.35 m above ground level.

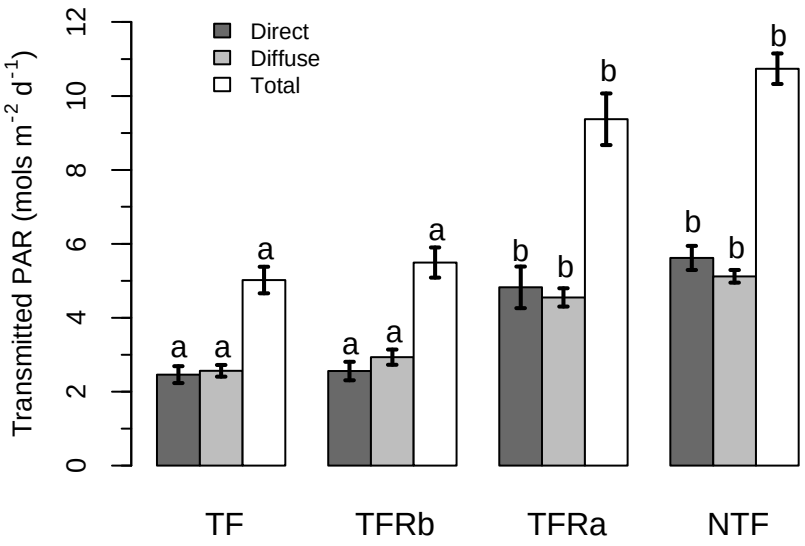


Figure 14. Mean direct, diffuse, and total transmitted photosynthetically active radiation (PAR) over the growing season at 1.35 m above ground level under mature *Pinus radiata* plantation canopy with either tree fern (TF) cover, before (TFRb) or after (TFRa) tree fern thinning, or in areas with no tree ferns (NTF). Experimental stands were five 36–92-year-old *P. radiata* plantations, located in Kaingaroa Forest, central North Island, New Zealand. The mean of each light transmission category was calculated from 15 hemispherical photographs in each tree fern status category. Columns of the same light transmission category with coinciding letters indicate no significant difference, whereas columns of the same light transmission category with different letters indicate significant differences at alpha = 0.05. Error bars represent ±1SE.

Tree fern thinning significantly increased transmitted PAR (Kruskal-Wallis rank-sum test, $H(3) = 22.712$, $P < 0.001$). Direct transmitted PAR was increased significantly after tree fern thinning ($P = 0.017$), from TFR_{before} = 2.6±0.3 mol m^{-2} d^{-1} to TFR_{after} = 4.8±0.6 mol m^{-2} d^{-1}. Diffuse transmitted PAR differed significantly among experimental treatments (Kruskal-Wallis rank-sum test, $H(3) = 39.43$, $P < 0.001$), and diffuse transmitted PAR increased significantly as a result of thinning ($P = 0.004$) from 2.9±0.2 mol m^{-2} d^{-1} to 4.6±0.3 mol m^{-2} d^{-1}. Total transmitted PAR differed significantly among experimental treatments (Kruskal-Wallis rank-sum test, $H(3) = 37.89$, $P < 0.001$). As a result of tree fern thinning, total transmitted PAR increased significantly ($P = 0.003$), from 5.5±0.4 mol m^{-2} d^{-1} to 9.37±0.7 mol m^{-2} d^{-1}. No significant difference occurred (all $P > 0.05$) in total transmitted PAR between TF and TFR_{before} treatments, nor between TFR_{after} and NTF treatments.

5.4.3. Seeding Growth Response

Podocarpus totara

Initial *P. totara* heights did not differ significantly among tree fern treatments (one-way ANOVA, $F2,42 = 0.406$, $P = 0.669$). At the end of the study, the proportional occurrence of *P. totara* seedling mortality was not significantly different ($P = 0.425$) among the tree fern treatments. Mean *P. totara* seedling mortality rates were 12.5±3% for TF, 7.1±2% for TFR, and 11.6±3% for NTF. A significant positive association was found between unbrowsed *P. totara* height growth and total transmitted PAR, at 1.35 m, among tree fern treatments (Simple Linear Regression, $F1,27 = 5.73$, $P = 0.024$, $R^2 = 0.18$; Fig. 16A).

Eighteen months after tree fern thinning, unbrowsed *P. totara* seedling RHG differed significantly (Kruskal-Wallis rank-sum test, $H(2) = 22$, $P < 0.001$) among treatments. Differences in mean unbrowsed *P. totara* RHG were significant where tree ferns had been removed (0.57±0.6 RHG, $P < 0.001$, 2.6-fold increase) or were not present (0.53±0.3 RHG, $P = 0.002$, 2.4-fold increase), compared to those from under tree fern cover (0.22±0.2 RHG). The difference in mean RHG between TFR and NTF treatments for unbrowsed *P. totara* was not significant ($P = 0.146$). Mean *P. totara* RHG for all seedlings (browsed and unbrowsed) among treatments was TF = 0.19±0.03 RHG, TFR = 0.34±0.08 RHG, and NTF = 0.34±0.7 RHG. Even though mean *P. totara* RHG in the TFR and NTF treatments were 1.8 times greater than those from the TF treatment (Fig. 17A), these differences were not statistically significant (Kruskal-Wallis rank-sum test, $H(2) = 4.712$, $P = 0.095$).

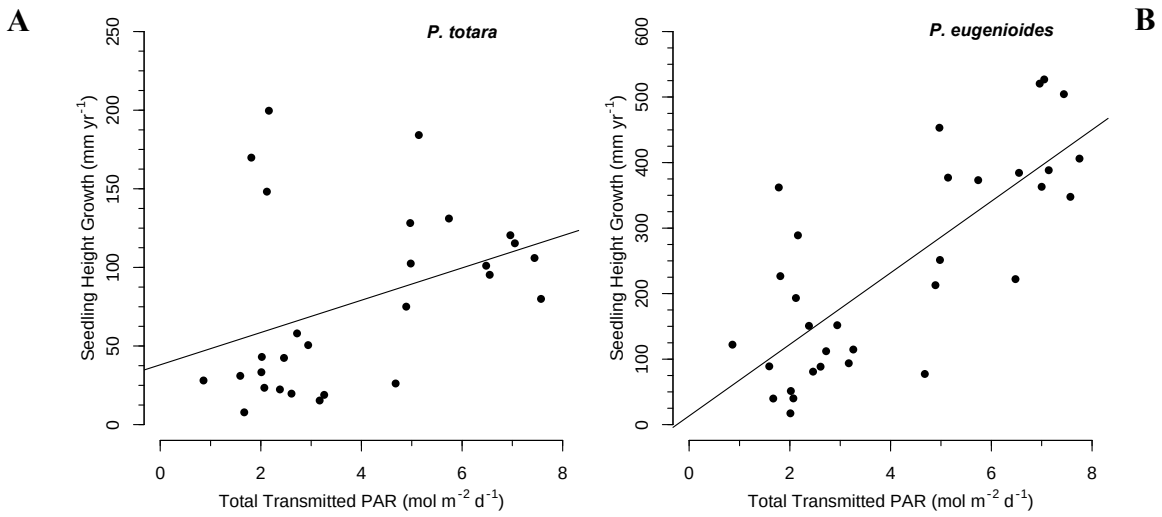


Figure 15. Per-annum scaled average seedling height growth per plot of unbrowsed (A) *Podocarpus totara* (n = 29), and (B) *Pittosporum eugenioides* (n = 32) as a function of total transmitted photosynthetically active radiation (PAR) measured within five *Pinus radiata* plantation stands, at 1.35 m above ground level, under different amounts of tree fern shading. Experimental stands were 36–92-year-old *P. radiata* plantations, located in Kaingaroa Forest, central North Island, New Zealand.

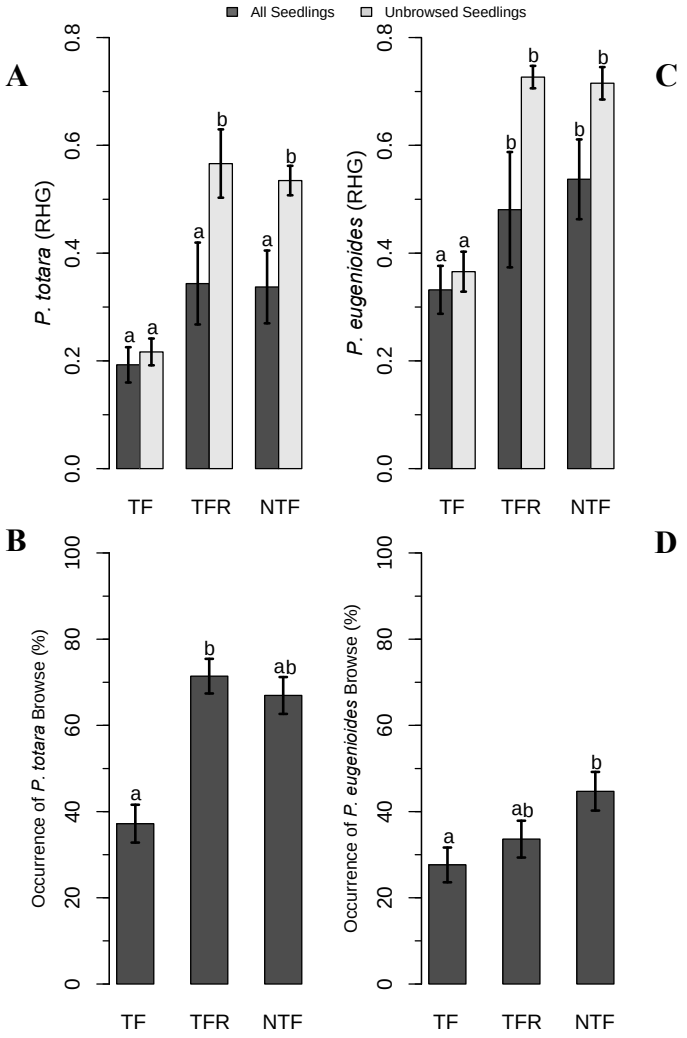


Figure 16. *Podocarpus totara* (A) relative height growth (RHG), (B) percentage occurrence of animal browse, *Pittosporum eugenioides* (C) RHG; and (D) percentage occurrence of animal browse. Seedling performance 18 months following experimental tree fern thinning within five 36–92-year-old *Pinus radiata* plantations, located in Kaingaroa Forest, central North Island, New Zealand. Sample sizes (plot means) for RHG "All Seedlings" and "Browse Occurrence" are each $n = 15$, for either species. RHG samples sizes (plot means) for "Unbrowsed Seedlings" are *P. totara*: TF $n = 14$, TFR $n = 8$, NTF $n = 8$; *P eugenioides*: TF $n = 14$, TFR $n = 8$, TFR $n = 10$. Columns with coinciding letters indicate no significant difference, whereas columns with different letters indicate significant differences at alpha = 0.05. Error bars represent ±1SE.

The proportional occurrence of animal browse differed significantly among treatments (Generalised Linear Model, $F2,42 = 3.66$, $P = 0.034$; Fig. 17B). The proportion of seedlings affected by animal browse was greatest in TFR treatments (71±4%) and was significantly greater ($P = 0.041$) than the occurrence of browse under tree fern cover (37±4%). While the occurrence of animal browse at sites with no tree ferns (67±4%) was similar to the TFR result, it was not significantly different from either TFR ($P = 0.934$) or TF ($P = 0.092$) treatments.

A significant interaction between tree fern treatment status and the occurrence of animal browse effected the relative height growth of all combined *P. totara* seedlings (Multiple Linear Regression, $F5,39 = 13.62$, $P < 0.001$, $R^2 = 0.636$, $R^2_{adjusted} = 0.589$). This significant tree fern × browsing interaction reflected the decreasing height growth in *P. totara* with increasing browse occurrence, with the most significant decrease in height growth found in the NTF treatment. These results indicate that all combined *P. totara* height growth in areas without tree ferns was dependent on the degree of animal browse.

Tree fern treatment status also explained a significant amount of the variance in the height growth of unbrowsed *P. totara* seedlings (Simple Linear Regression, $F2,26 = 31.23$, $P < 0.001$, $R^2 = 0.71$). All three tree fern treatments were significant predictors of unbrowsed *P. totara* seedling height growth, and unbrowsed *P. totara* height growth was positively associated with tree fern removal (TFR, $\beta = 52.46$, $P = 0.041$) or clearings amongst tree ferns (NTF, $\beta = 153.88$, $P < 0.001$), and negatively associated with the presence of tree ferns (TF, $\beta = -108.85$, $P < 0.001$).

Pittosporum eugenioides

Initial *P. eugenioides* heights did not differ significantly among tree fern treatments (one-way ANOVA, $F2,42 = 0.207$, $P = 0.814$). At the end of the experiment there were no significant differences ($P = 1.00$) in the proportion mortality of *P. eugenioides* seedlings among experimental treatments. The mean percentage mortality rates for experimental treatments were 9.8±2.6% for TF, 10.7±2.7% for TFR, and 9.7±2.6% for NTF. A significant positive association was found among tree fern treatments between *P. eugenioides* height growth and the total transmitted PAR at 1.35 m (Simple Linear Regression, $F2,30 = 44.4$, $P < 0.001$, $R^2 = 0.60$; Fig. 17B).

Mean unbrowsed *P. eugenioides* RHG were significantly different (Kruskal-Wallis rank-sum test, $H(2) = 22.919$, $P < 0.001$) among treatments. Unbrowsed *P. eugenioides* growing under tree fern cover (0.37±0.04 RHG) achieved significantly less RHG than those seedlings from either the TFR (0.73±0.02 RHG, $P < 0.001$, 2-fold increase) or NTF (0.72±0.03 RHG, $P < 0.001$, 1.9-fold increase) treatments. Mean seedling RHG of the TFR and NTF treatments did not differ significantly ($P = 0.656$). All combined *P. eugenioides* seedling RHG differed significantly among treatments 18 months after tree fern thinning (Kruskal-Wallis rank-sum test, $H(2) = 12.049$, $P = 0.002$; Fig. 17C). All combined *P. eugenioides* RHG were significantly different between TF (0.33±0.04 RHG) and both TFR (0.48±0.11 RHG, $P = 0.010$, 1.5-fold increase) and NTF (0.54±0.07 RHG, $P = 0.006$, 1.6-fold increase) treatments. The difference in the means of all combined *P. eugenioides* RHG between TFR and NTF was not significant ($P = 0.985$).

The occurrence of animal browse differed significantly ($P = 0.019$) among tree fern treatments. A significantly greater ($P = 0.023$) proportion of *P. eugenioides* seedlings were affected by animal browse in the NTF (45±0.5%) treatment compared to the TF (27.6±0.4%) treatment (Fig. 17D). Any other difference in the proportion of animal browse among treatments was not significant (all $P > 0.17$).

Tree fern treatment status and the occurrence of animal browse explained a significant amount of the variance in the relative height growth of all combined *P. eugenioides* seedlings (Multiple Linear Regression, $F5,39 = 34.42$, $P < 0.001$, $R^2 = 0.815$, $R^2_{adjusted} = 0.792$). The occurrence of animal browse was a marginally significant ($P = 0.063$) and negatively associated ($\beta = -21.18$) predictor of all combined *P. eugenioides* height growth. Significant interactions occurred for both TFR and NTF treatments with animal browse occurrence, suggesting the height growth of *P. eugenioides* in areas cleared of tree ferns, or within existing clearings, would be dependent on the extent of animal browse.

Tree fern treatment status also explained a significant amount of the variance in the height growth of unbrowsed *P. eugenioides* seedlings (Simple Linear Regression, $F2,29 = 38.71$, $P < 0.001$, $R^2 = 0.73$). Both NTF ($\beta = 532.28$, $P < 0.001$) and TF ($\beta = -400.60$, $P < 0.001$) treatments were significant predictors of *P. eugenioides* seedling height growth.

5.5. DISCUSSION

5.5.1. Woody Seedling Performance Among Dense Tree Fern Stands in *P. radiata* Plantations

Internationally, plantation forests have been found to serve a facilitative nursery function for indigenous forest regeneration (Brockerhoff et al., 2008a; Parrotta et al., 1997) and, in particular, non-harvest plantations provide a potential pathway for restoration of indigenous forest communities (Paquette & Messier, 2009; Lamb, 1998). However, our results support the view that tree fern dominated plantation forest understories can significantly reduce seedling growth rates of indigenous canopy tree species, thereby limiting forest regeneration (cf. Coomes et al., 2005; George & Bazzaz, 1999). Therefore, where tree ferns are a dominant feature of plantation understories, it is important to understand both the role of tree ferns in limiting natural regeneration where an indigenous seed source is available, and how tree fern stands might be manipulated to promote the restoration process.

As predicted, tree fern removal significantly increased canopy openness and transmitted PAR, and resulted in significant increases in the growth rate of both *P. totara* and *P. eugenioides* seedlings. After 18 months, unbrowsed seedlings at sites cleared of tree ferns achieved significantly greater heights (*P. totara* = 0.57±0.6 RHG, *P. eugenioides* = 0.73±0.02 RHG) than those located under tree fern cover *(P. totara* = 0.22±0.2 RHG, *P. eugenioides* = 0.37±0.04 RHG). This then suggests that dense tree fern stands within New Zealand *P. radiata* plantations may present significant limitations on indigenous canopy tree seedling growth. Where *P. radiata* plantations are to be optimized for indigenous forest restoration outcomes, and areas of dense tree fern understorey exist, tree fern control will need to be considered.

As expected, compared to *P. totara*, *P. eugenioides* grew faster and had a stronger positive association with the increased illumination (Fig. 16B) caused by tree fern removal. As an indicative comparison, the *P. totara* growth rates under tree fern cover, or where tree ferns were removed but animal browse occurred, would be insufficient to compete with the mean *D. squarrosa* growth rate of 48 mm year^{-1} (43.1–53.7 95%CI), found by the study of an indigenous podocarp-broadleaved forest located near Wellington, New Zealand (Bystriakova et al., 2011).

The competitive balance between species is ultimately dependent on the respective life history traits (Walker, 1994). As well as reducing light quantity, dense tree fern cover is likely to alter light quality, causing a tendency towards far red enrichment resulting from red light absorption by the shading plants (Franklin, 2008). In response to these modifications of the light environment, species will differ in their competitive abilities according to shade tolerance and growth rate related life history traits. Our results suggest that the shade tolerance growth rate related life history traits of *P. totara* are incompatible with the heavily shaded environment created by dense tree fern stands under the *P. radiata* canopy. However, the early successional *P. eugenioides* showed considerably faster growth rates that would likely be more competitive with those of *D. squarrosa*.

The influential role that animal browsers have in this forest succession is highlighted by both the significant browse occurrence × TFR/NTF treatment status interactions, and the significantly higher rates of mammalian animal browse where tree ferns were removed (*P. totara*), or in clearings with no tree ferns (*P. eugenioides*). Preferential foraging by ungulates in the high-light environments of forest clearings is known from European temperate forests (Kuijper et al., 2009), and the higher nutrient content of foliage in higher-light environments may promote animal browse (Coomes et al., 2003). Animal browse diminished any significant benefit of tree fern removal on *P. totara* height growth, whereas for *P. eugenioides*, the comparatively lower browse occurrence, coupled with faster growth rates, meant significant height growth differences were achieved even when browsed seedlings were taken into account (Fig. 16C). The tree fern species present in our study are unpalatable and either not selected or avoided by introduced mammalian browsers (Forsyth et al., 2002). Our results suggest that seedling attributes regarding shade tolerance, growth rate, and palatability are important seedling life history traits in this highly competitive successional stage of tree fern dominance.

5.5.2. Tree Fern Dominated Understories of Central North Island *P. radiata* Plantations

Tree ferns may exhibit habitat selection according to shade-tolerance-related life history traits (Bernabe et al., 1999; Bittner & Breckle, 1995) and are known to invade and dominate recently disturbed, high-light environments. In Mexican cloud forest, tree fern survival and growth differed between forest edge and interior habitats (Bernabe et al., 1999), and within Costa Rican premontane wet forest, tree fern trunk growth rates were found to be influenced

by habitat; *Cyathea delgadii* grew at three times the rate within secondary forest as it did in primary forest (Bittner & Breckle, 1995). Within Colombian cloud forest, tree ferns colonised disturbed sites, with tree fern densities significantly greater on abandoned pasture and secondary forest compared to primary forests (Arens & Baracaldo, 1998).

Our tree fern stands are of a similar total tree fern trunk density (TF = 2153±260 stems ha^{-1}, TFR_{before} = 1977±327 stems ha^{-1}) and basal area to those measured by Ogden et al. (1997) in central North Island *P. radiata* forests of similar age (2000–2500 stems ha^{-1}). From both studies, total tree fern stem densities in exotic *P. radiata* plantations are more than two-fold greater than those in New Zealand indigenous forests (*ca.* ≤ 1000 stems ha^{-1} (Druitt et al., 1990); 600.9 stems ha^{-1} (Bystriakova et al., 2011)).

The mature *P. radiata* plantation canopies create a relatively high-light environment for forest understorey development. Where tree ferns were cleared, the *P. radiata* canopy transmitted, on average, 28±2% PAR, which is high compared to transmitted PAR levels from previous studies from New Zealand's temperate podocarp-broadleaved forests: where values were 1.3–5.2% (McDonald & Norton, 1992), 4.9–29.4% (Ebbett & Ogden, 1998), 0.55–6% (Davies-Colley et al., 2000), and 0.3–24% (Lusk et al., 2009). Within *P. radiata* plantations of the central North Island, *Cyathea* and *Dicksonia* tree ferns rapidly colonize the understorey, expanding in cover over the period 20–40 years after plantation establishment (Brockerhoff et al., 2003; Ogden et al., 1997; Allen et al., 1995). A particular feature of this tree fern community is the dominance by *D. squarrosa* (occupies *ca.* 85% of the tree fern composition in this study, and 84% in Ogden et al. (1997)). With its vegetative reproduction and its rhizomatous spreading ability, *D. squarrosa* rapidly forms large, heavily-shaded colonies within the *P. radiata* understorey. As found for other tree fern species in forests subjected to clear-fell harvest operations (Ough & Murphy, 2004), *D. squarrosa* can persist between forest rotations by vegetative reproduction from trunks surviving plantation clear-felling and reestablishment, thereby allowing its early establishment and boosting its ability to rapidly dominate understorey composition within recently clear-felled *P. radiata* stands (Ogden et al., 1997; Allen et al., 1995).

Factors additional to the strongly competitive shading effects of tree ferns might also contribute to tree fern dominance in this central North Island *P. radiata* succession. We found that introduced mammalian browsers had a significant influence on these forest understories by suppressing the height growth rates of indigenous canopy tree seedlings. Other studies

have found that the preferential animal browse of woody seedlings over unpalatable ferns (Nuttle et al., 2014; De la Cretaz & Kelty, 2002) and tree ferns (Rogers & Leathwick, 1997; Campbell, 1990; Jane & Pracy, 1974) led to effective regeneration, and ultimately dominance, by only the unpalatable fern species. In our *P. radiata* stands, preferential browse would equate to a selection on regeneration in favor of tree fern dominance and persistence over indigenous forest canopy tree species.

While we suggest light would have the strongest effect on seedling growth, tree fern removal might also affect other factors relevant to seedling growth in *P. radiata* understories, such as the degree of belowground competition, rainfall interception, or nutrient release arising from vegetation removal. On the island of Hawai'i, a trenching experiment found that increased root competition from the invading *Myrica faya* (Myricaceae) reduced seedling growth rates of the dominant forest tree species, *Metrosideros polymorpha* (Myrtales) (Walker & Vitousek, 1991). Our experiment did not address belowground competition, and we suggest there is scope for further research into the effects of belowground competition on indigenous forest regeneration within tree fern dominated plantation understories. Although it is conceivable that the dense tree fern cover might limit water availability to seedlings by intercepting rainwater during light precipitation events (Padilla & Pugnaire, 2006), in this relatively wet climate (mean annual rainfall is 1480 mm) we do not expect rainfall interception by tree fern cover to have had a large effect on seedling growth performance. We note that vegetation removal experiments can cause a nutrient release, and this presents a potentially confounding effect on seedling growth, by increasing seedling shade tolerance. However, in our experiment both *P. totara* and *P. eugenioides* growth responses were similar between TFR and NTF treatments, and this then suggests that there was no nutrient related confounding effect on seedling growth caused by tree fern removal.

5.5.3. Methods of Promoting a Woody Succession

Our experimental stands were aged 36–92 years, with high densities of tree ferns, suggesting tree fern dominated *P. radiata* understories in this area might persist for five decades or more. While not formally surveyed, our stands showed limited evidence of woody indigenous forest successions, signaling an absence of substantial competition by woody species within the existing tree fern dominated understorey community.

While our seedling growth rates for *P. totara* and *P. eugenioides* provide evidence that tree fern stands significantly reduce indigenous canopy tree seedling height growth, we note that mature indigenous canopy tree seedlings may not always be able to establish themselves amongst dense tree fern stands within *P. radiata* plantations. In addition to heavy tree fern shade (Coomes et al., 2005; George & Bazzaz, 1999) and selective favoring of unpalatable tree ferns by mammalian browsers, the establishment of indigenous canopy tree species might be limited by a number of factors. These include: disrupted propagule dispersal due to ecological isolation (Hewitt & Kellman, 2002; Zanne & Chapman, 2001), the physical interruption of indigenous forest seed rain reaching the forest floor due to the heavy tree fern frond cover, or the difficulty of seedling establishment in the dry, deep litter layer that occurs under tree ferns (cf. Walker, 1994). We suggest seedling establishment might also be limited because of the replacement of mineral substrates by organic fibrous root mats associated with established *D. squarrosa* stands.

In order to promote indigenous woody successions within *P. radiata* stands with dense tree fern growth, interventions such as cutting, uprooting or herbicide application (De la Cretaz & Kelty, 2002) should be considered to reduce the competitive effects of tree ferns and to provide establishment sites for indigenous canopy species representative of local natural forests to competitively shade the forest floor. Where indigenous forest seed sources are distant, underplanting might be a necessary intervention to incorporate mature canopy species into the forest succession (Lamb et al., 2005). Within our study area, we have also found that underplanting of indigenous conifers (podocarps) under a degraded *Pinus ponderosa* canopy that had been opened by fungal pathogen attack accelerated forest succession by establishing structural dominance of a long-lived mature forest canopy species within only 50 years (Forbes et al., 2015). Underplanting plantation understories to incorporate late-successional species has also been successful in Sri Lankan *Pinus caribaea* plantations (Ashton et al., 1997), as well as in Spanish (Rodriguez-Calcerrada et al., 2008) and German (Noack, 2011) *Pinus sylvestris* plantations.

Given our results of increased animal browse within tree fern clearings, mammalian animal control in cleared areas is also important in order to maximize seedling growth rates. As an alternative to costly traditional animal control techniques, protection of regeneration from browsers in small plantation forest clearings has been successfully achieved through use of forest slash barriers, physically preventing access by browsers to seedlings within clearings

(Kota & Bartos, 2010; de Chantal & Granstrom, 2007; Rumble et al., 1996). We suggest this as a potential restoration technique in central North Island plantation forests, and where this involves felling canopy trees this treatment may provide complementary opportunities to optimise the understorey light environment for forest regeneration through creation of small-scale canopy gaps (Lamb et al., 2005).

Our results suggest that where clearings are created, in order to out-compete the competitive fern regrowth within these *P. radiata* stands, faster-growing, light-demanding species of low palatability would be the best option for overcoming the competitive effects of tree fern re-invasion of cleared sites. This study demonstrates that alleviating the tree fern competition enhances establishment of late-successional species in central North Island exotic *P. radiata* plantation forests.

5.6. CONCLUSIONS

Where tree ferns are a dominant understorey feature of non-harvest plantation forests, the deep shade associated with these ferns is likely to reduce the plantation's restoration potential. Dense tree fern stands significantly reduced the seedling height growth rates of the indigenous forest canopy species *P. totara* and *P. eugenioides*, within central North Island exotic *P. radiata* plantations, thus limiting the potential succession towards indigenous forest. Life history traits regarding shade tolerance and growth rates explain the differences in the competitiveness of *P. totara* and *P. eugenioides* seedlings in these tree fern dominated forest understories. The common occurrence of animal browse by introduced mammals suggests palatability is also an important factor influencing seedling regeneration within these plantation forests. Faster-growing, light-demanding species of low palatability would be the best candidates for inclusion in the current tree fern dominated phase of forest succession when the goal is restoration of indigenous forest. Our results show that where dense tree fern stands occur, intervention can promote a woody indigenous succession. The physical clearance of tree fern stands and then the establishment of fast-growing indigenous canopy tree species of low palatability, are suggested restoration strategies. Protection from animal browse should also be considered.

6. CHAPTER FIVE:

Underplanting Degraded Exotic *Pinus* with Indigenous Conifers Assists Forest Restoration

CHAPTER PREFACE

Chapter Two highlighted the importance of proximity to indigenous forest seed sources for woody species richness, woody vegetation structure, and the composition of indigenous understorey regeneration within *P. radiata* plantations. *Pinus radiata* stands located in close proximity to natural forest contained mature forest canopy species that were only in low numbers, or were absent, in more ecologically isolated stands, regardless of stand age. Chapter Three found that the creation of small-scale canopy gaps in *P. radiata* plantation forest increased understorey light levels, and provide a means of optimising light conditions for the growth of mature forest canopy species planted into *Pinus* plantation forest. Chapter Four also concluded that growth rates of mature forest canopy species within *Pinus* plantations can be significantly affected by dense vegetation cover, the example given in Chapter Four was dense tree fern cover in central North Island plantation understories.

Chapter Five builds on the findings of these previous chapters by addressing the constraints on indigenous forest regeneration in exotic *Pinus* stands presented by ecological isolation from indigenous forest seed sources. Chapter Five incorporates the findings from Chapters Three and Four in the sense that the survey is undertaken in a degraded *Pinus* plantation where canopy cover has been reduced through pathogen attack, thereby increasing light transmission to the forest understorey. Chapter Five presents an investigation into the potential for underplanting of *Pinus* plantations with mature forest canopy species to direct and accelerate successional development toward indigenous dominance.

Chapter Five was published in the journal Ecological Management and Restoration. My Supervisors, Prof. David Norton and Dr. Fiona Carswell, are co-authors of the manuscript. This paper is enclosed as Appendix E, and the citation for the paper is:

Forbes, A. S., Norton, D. A., & Carswell, F. E. (2015). Underplanting degraded exotic *Pinus* with indigenous conifers assists forest restoration. *Ecological Management and Restoration, 16*(1), 41–49.

The vegetation history and background information regarding the underplanting trial were published as supplementary information and this information is enclosed as Appendix G. Carbon storage calculations were also submitted as supplementary information and this information is enclosed as Appendix H.

6.1. ABSTRACT

We propose that non-harvest plantations could provide important opportunities for restoration of indigenous forest cover and related ecosystem services. We assessed the relative performance of three Podocarpaceae (podocarps) species planted into a degraded Ponderosa Pine (*Pinus ponderosa*) plantation, central North Island, New Zealand. We hypothesised that the degraded pine plantation overstorey could provide suitable conditions for the development of a podocarp dominated forest structure within *ca*. 50 years of underplanting, and that podocarp growth would differ depending on the species suitability to the site.

Rimu (*Dacrydium cupressinum*) significantly outperformed both Totara (*Podocarpus totara*) and Kahikatea (*Dacrycarpus dacrydioides*) in height and diameter growth. Rimu was now the structurally dominant tree where it occurred rather than pine. Per annum scaled carbon storage within Rimu stands was significantly greater than the Totara, Kahikatea, or Pine stands. All podocarp species had attained a greater stand density compared to the pine overstorey. Possible reasons for the differing podocarp growth performance include different light requirements, response to soil nutrients, elevational distributions, and frost susceptibility. There were significant differences in understorey species richness among the different stands of podocarp species.

Underplanting accelerated successional development by incorporating late successional indigenous canopy dominants within the forest succession and overcame limitations imposed on forest succession at the site from its isolation from indigenous forest tree seed sources.

6.2. INTRODUCTION

New Zealand has lost 71% (i.e., 14 million ha) of its former indigenous forest cover (Ewers et al., 2006) which has led to dramatic reductions in provision of indigenous biodiversity and forest derived ecosystem services, such as carbon storage. The contemporary land cover of New Zealand includes *ca*. 7% (1.73 million ha) of exotic plantation forest and over 90% of this comprises Radiata Pine (*Pinus radiata*) (Ministry of Primary Industries [MPI], 2013). Under New Zealand conditions pine plantation growth is rapid, typically reaching commercial maturity within 25–30 years from establishment. Changes in social and economic circumstances over the lifetime of a plantation forest mean that management objectives for plantation stands can change (Lamb, 1998). Harvesting may be abandoned for economic, environmental, or social reasons leading to plantations that are retained on the landscape for non-harvest purposes. Considering the pioneering attributes of pine species grown in commercial plantations, coupled with the potential national distribution of non-harvest stands, we propose that non-harvest plantations could provide important opportunities for the restoration of indigenous forest cover in New Zealand.

Underplanting plantations with indigenous species for forest restoration is widely recognised internationally as a means of initiating and establishing successional processes (Weber et al., 2011; Paquette et al., 2006; Lamb et al., 2005). Underplanting is of particular benefit at sites where seed rain is disrupted due to isolation from seed sources and where underplanted trees themselves attract seed dispersing birds into the forest and serve as a catalyst for successional development (Weber et al., 2011). There are numerous examples of pine plantations that have been underplanted with native species for forest restoration outcomes. For example, species of the genera *Fraxinus*, *Pinus*, and *Quercus* were successfully established within young *Pinus* plantations in Canada to assist natural succession (Parker et al., 2001), as was *Pinus* in the United States (Knapp et al., 2013; Gilmore, 2000), and *Quercus* in Spain (Rodriguez-Calcerrada et al., 2008) and in Germany (Noack, 2011). In Sri Lanka underplanting *Pinus* plantations was found to be a successful way of introducing late-successional tropical rainforest tree species to the forest succession for restoration purposes (Ashton et al., 2001).

Here we assessed the potential of underplanting as a management tool to facilitate indigenous forest development under a plantation canopy in New Zealand. We did this by measuring the performance of three Podocarpaceae conifers planted into the shelter of an

already degraded pine plantation on the Kaingaroa Plateau, central North Island. We surveyed tree and understorey composition of a long-term Forest Research Institute (FRI) plantation underplanting trial approximately 50 years after trial establishment. Underplanted species assessed were the endemic trees Totara (*Podocarpus totara*), Kahikatea (*Dacrycarpus dacrydioides*), and Rimu (*Dacrydium cupressinum*). These species are ubiquitous New Zealand forest trees that have important roles in the provision of biodiversity and storage of carbon within many of New Zealand's podocarp-broadleaved forests. Totara and Kahikatea are both light demanding species (Ebbett & Ogden, 1998; Ogden & Stewart, 1995; McKelvey, 1963; Cameron, 1960) while Rimu is regarded as more shade tolerant (Ogden & Stewart, 1995; Bartlett, 1984). Growth of Totara and Kahikatea is more rapid on fertile sites (Leathwick, 1995), while Rimu is more competitive on infertile sites (Leathwick, 1995; Hawkins & Sweet, 1989). The three podocarp species have different elevational distributions (Bergin, 2000; Norton et al., 1988), with Rimu naturally ranging to comparatively higher elevation sites (Norton et al., 1988). Totara is more susceptible to frost than Kahikatea (Beveridge et al., 1973), yet both species are less tolerant of frost than Rimu (Sakai et al., 1981; Beveridge et al., 1973).

We hypothesise that a degraded pine plantation overstorey can provide suitably sheltered conditions for the development of a podocarp cohort to the extent that an indigenous dominated forest structure is achievable within *ca.* 50 years of underplanting. We expect the shaded conditions created by the degraded plantation, the relatively low nutrient soils, together with the elevated and frost prone nature of the trial site will favour Rimu growth over either Totara or Kahikatea. We examine the composition of the forest understorey that develops within an entirely planted production forest in this location, and the influence underplanting species choice has on that composition.

6.3. METHODS

6.3.1. The Study Area

The study area is located in the northern portion of the Kaingaroa Plateau, central North Island, New Zealand (38°22'32"S 176°31'13"E) and comprises a 12.5 ha plantation stand of Ponderosa Pine (*Pinus ponderosa*). The site is at 520 m above sea level (a.s.l.), on flat topography. The area comprises ignimbrite rock layers that have resisted erosion to retain a plateau landform (Vucetich et al., 1960). Soils are derived from rhyolitic pumice ash deposits

originating from the Taupo (*ca*. 1700 years ago) and Kaharoa (*ca*. 800 years ago) eruptions (Vucetich et al., 1960). Soils are Te Rere shallow sand—a thin, light, free-draining soil overlying white pumice sand and gravel. The Te Rere shallow sand is of low drought vulnerability (S-map, 2014) and is leached and relatively low in plant nutrients. The trial site soils have a C:N ratio of 19 (± 0.17 SEM).

Rainfall is distributed evenly throughout the year (Vucetich et al., 1960), with an annual mean (1914 – 1999 mean measured at the Kaingaroa Village Climate Station, located *ca*. 5 km to the south-east of the trial site) of 1,480 mm (National Institute of Water and Atmospheric Research [NIWA], 2013). Rain falls (> 1 mm of rain) on 8–13 days of any month of the year. The annual mean temperature is 11°C (January mean 16°C; July mean 5°C). Maximum daily January temperatures average 22°C and the minimum daily July temperatures average -0.4°C.

Frosts are a significant component of the site's climate. In this northern, relatively lower elevation area of the Kaingaroa Plateau frosts can occur over 10 months of the year (March–December) but are more frequent from May–September. Frosts are most frequent in July, occurring on an average (1958–1994 mean) of 14 days of that month. Air temperatures as cold as -9.4°C have been recorded during July at the Kaingaroa Village Climate Station, and temperatures can typically drop to -3 – -4°C during winter and early spring (NIWA, 2013).

6.3.2. Podocarp Underplanting Trial

The underplanting trial was established in 1962 within a Ponderosa Pine stand that was established in 1926. The plantation was affected by a *Dothistroma pini* (fungal pathogen) outbreak that degraded the plantation by thinning the canopy. Canopy cover declined from 20–30% cover in 1975, to 10% cover in 1987, and to the < 5% cover today (2013). In 1962 a total of 8,900 Totara, 8,900 Kahikatea, and 6,250 Rimu were planted in separate stands at the trial site (Pardy, 1987). Trial establishment incorporated one *ca*. 14 × 60 m plot within each podocarp stand. No control (planted podocarps without pine overstorey) plots were established, although podocarps do not perform well, especially at frost prone sites similar to the study site, without a vegetative nurse (Franklin, 1968; Cameron, 1960) and therefore a control comprising open planted podocarps would not have been viable at this locality. Although each podocarp species was only planted within a single stand, topography and climate are very similar and soil C:N ($H(2) = 5.92$, $p = 0.052$) was not significantly different

among the three stands. Contemporary mean Ponderosa Pine basal area ($F(2,9) = 0.66$, $p = 0.54$) and stem density ($F(2,9) = 1.01$, $p = 0.40$) also did not differ significantly between the three stands, providing further evidence that environmental conditions at the trial site are homogenous. A description of the historical vegetation of the trial site and further description of the underplanting trial are presented in Appendix G.

6.3.3. Field Survey

Four replicate 10 × 10 m understorey vegetation plots were randomly positioned within each of the three podocarp stands (12 plots in total). A minimum 25 m separation distance between plots was used to avoid overlap among plots. The original survey plots measured in the earlier FRI surveys of the trial were integrated into the current survey by randomly locating one understorey plot, per podocarp species, within the original plot. A 0.03 ha circular quadrat was centred on each understorey plot to survey canopy trees. To avoid edge effects, a 20 m buffer around the plantation edge was excluded from the area available for random positioning of plots. Trees were defined as > 2.5 cm trunk diameter at a height of 1.35 m (i.e., diameter at breast height; DBH). The basal area results presented relate to specific tree species, rather than a mix of all tree species from survey plots.

Understorey vascular plant cover and vertical height structure were surveyed using the RECCE method within each 10 × 10 m plot (Hurst & Allen, 2007). Cover-abundance for each understorey species was estimated using the scale: 1 = <1%, 2 = 1–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75%, 6 = 76–100%. Understorey species were recorded when they had live foliage present in height tiers: >25 m, 12–25 m, 5–12 m, 2–5 m, 0.3–2 m, <0.3 m. Presence of epiphytes was recorded separately. Height and diameter of all live canopy trees (pines and podocarps) within 0.03 ha canopy tree plots were recorded. Tree height measurements were made using a Vertex III hypsometer. Plant nomenclature follows the New Zealand Plant Conservation website (www.nzpcn.org.nz, accessed 13 May 2014).

Soils were surveyed to determine any significant differences among podocarp stands. From the soil A Horizon eight randomly located 15 cm soil cores were bulked from eight regions of each podocarp stand. Soil samples were subsampled, coarse sieved, and dried at 40°C for 14 hours, before being sieved to 1 mm and analysed for Total Carbon and Total Nitrogen, following the Dumas method.

6.3.4. Statistical Analyses

Mean growth performance values were compared using one-way ANOVA or Student's *t*-test. Where statistically significant differences at $p \leq 0.05$ were found, pairwise post-hoc comparison using Tukey's honest significance difference (HSD) was used to test for statistically significant differences among sample means. Kruskal–Wallis rank sum test was used to test for differences in soil quality among podocarps stands. The above statistical analyses were performed using R (R Development Core Team, 2013). Error estimates represent one standard error of the mean, which were calculated in R using the 'Plotrix' package. The method for calculation of carbon storage is presented in Appendix H.

Forest understorey species 'importance values' (IV) were calculated following Allen et al. (1995). The following weights were allocated to the RECCE cover-classes (cover-class = weight): 1 = 1.0, 2 = 2.0, 3 = 3.0, 4 = 4.0, 5 = 5.0, 6 = 6.0. Epiphytes were given a nominal weighting of 0.5. The IV for each species present within the plot was then calculated by summing the weighted cover-abundance score for the different tiers the species was recorded in. This analysis resulted in understorey species IV ranging from 0.5–15.0.

Inferences regarding compositional differences in understorey flora among podocarp stands were made with Non-Metric Dimensional Scaling (nMDS) using the metaMDS function in the R Vegan package (maximum of 20 iterations, in two dimensions). Similarity percentage analysis (SIMPER) was used to assess which taxa were primarily responsible for an observed dissimilarity among site groups (Clarke, 1993). SIMPER is based implicitly on Bray-Curtis dissimilarity and was used here for pairwise comparison of understorey composition among Totara, Kahikatea, and Rimu stands. Taxa with a high level of contribution to among stand dissimilarity, and with low standard deviation, are consistently responsible for differences in understorey composition among podocarp stands (Clarke, 1993). Similarity percentage was calculated using the SIMPER function in the R Vegan package. Permutational multivariate analysis of variance was used to determine the significance of differences in understorey composition among podocarp stands, using the Adonis function in the R Vegan package.

6.4. RESULTS

6.4.1. *Pinus* Plantation Stature

Eighty-seven years after establishment, the Ponderosa Pine stand had a mean canopy top height of 17.3 m (± 0.53 m), a mean basal area of 12.9 $m^2 ha^{-1}$ (± 1.93 $m^2 ha^{-1}$), and a mean live stem density of 205.6 stems ha^{-1} (± 31.2 stems ha^{-1}). Approximately 56% (n = 95) of all remaining plantation trees (n = 170) were dead standing. Consequently, the plantation canopy was sparse, with Ponderosa typically comprising < 5% total canopy cover.

6.4.2. Podocarp Stature and Relative Growth Performance

After 51 years of growth, height varied significantly among the three podocarp species (F(2,9) = 8.141, P = 0.009) (Fig. 18A). Rimu (11.5 ± 0.25 m) were significantly taller than Kahikatea (10.0 ± 0.09 m), but there was no significant difference between the heights of Totara (10.6 ± 0.36 m) and Kahikatea, nor between those of Rimu and Totara (Fig. 18A). The mean annual increment (MAI) height growth also varied significantly among the three podocarp species (F(2,9) = 8.195, P = 0.009) (Fig. 18B). Rimu (0.226 ± 0.005 m) had significantly greater MAI height growth than Kahikatea (0.197 ± 0.002 m), but not Totara (0.209 ± 0.007 m). There was no significant difference between the MAI height growth of Totara and Kahikatea. However, the better performing (upper quartile) Totara (0.255 ± 0.009 m), Kahikatea (0.246 ± 0.002 m), and Rimu (0.247 ± 0.004 m) were not significantly different with regard to MAI height growth (Fig. 18C).

DBH varied significantly among the three podocarp species (F(2,9) = 55.45, P = < 0.001) (Fig. 18D). Rimu (20.1 ± 0.50 cm) were significantly larger than either Totara (15 ± 0.56 cm) or Kahikatea (13.1 ± 0.38 cm). Totara and Kahikatea diameter were also significantly different. The three podocarp species varied significantly in MAI diameter growth (F(2,9) = 55.90, P = < 0.001) (Fig. 18 E). Rimu (0.395 ± 0.010 cm) had a significantly larger MAI diameter growth than either Totara (0.295 ± 0.011 cm) or Kahikatea (0.257 ± 0.007 cm) but the MAI diameter growth of Totara and that of Kahikatea were not significantly different. The most rapidly growing (upper quartile) podocarps varied significantly in MAI diameter growth (F(2,9) = 19.21, P = < 0.001) (Fig. 18 F). Upper quartile Rimu (0.529 ± 0.026 cm) had a significantly higher MAI diameter than either Totara

(0.432 ± 0.019 cm) or Kahikatea (0.372 ± 0.005 cm). The better performing Totara and Kahikatea did not vary significantly in MAI diameter.

Stand density did not differ significantly among the three podocarp species (Fig. 19A), but basal area did ($F(2,9) = 13.14$, $P = 0.002$) (Fig. 19B). Rimu (16.5 ± 2.11 m^2 ha^{-1}) had a significantly greater basal area than either Kahikatea (7.1 ± 0.89 m^2 ha^{-1}) or Totara (7.0 ± 1.28 m^2 ha^{-1}). The difference in basal area between Kahikatea and Totara was not significant.

Podocarps varied significantly in their respective C-stocks ($F(2,9) = 22.23$, $P = < 0.001$) (Fig. 19C). Rimu (32.3 ± 3.87 t ha^{-1}) had attained greater mean C-stock than either Totara (11.5 ± 2.15 t ha^{-1}) or Kahikatea (10.2 ± 1.11 t ha^{-1}), and had a similar mean C-stock value to that of the pine located within the Rimu stand (31.7 ± 7.79 t ha^{-1}). Carbon stocks of Totara and Kahikatea were similar. Rimu (0.64 ± 0.08 t C ha^{-1} $year^{-1}$) significantly ($F(3,44) = 28.96$, $P = < 0.001$) out performed Kahikatea (0.19 ± 0.02 t C ha^{-1} $year^{-1}$), Totara (0.23 ± 0.04 t C ha^{-1} $year^{-1}$), and also the pine stand (0.30 ± 0.06 t C ha^{-1} $year^{-1}$) with regard to C-stock per annum (Fig. 19D).

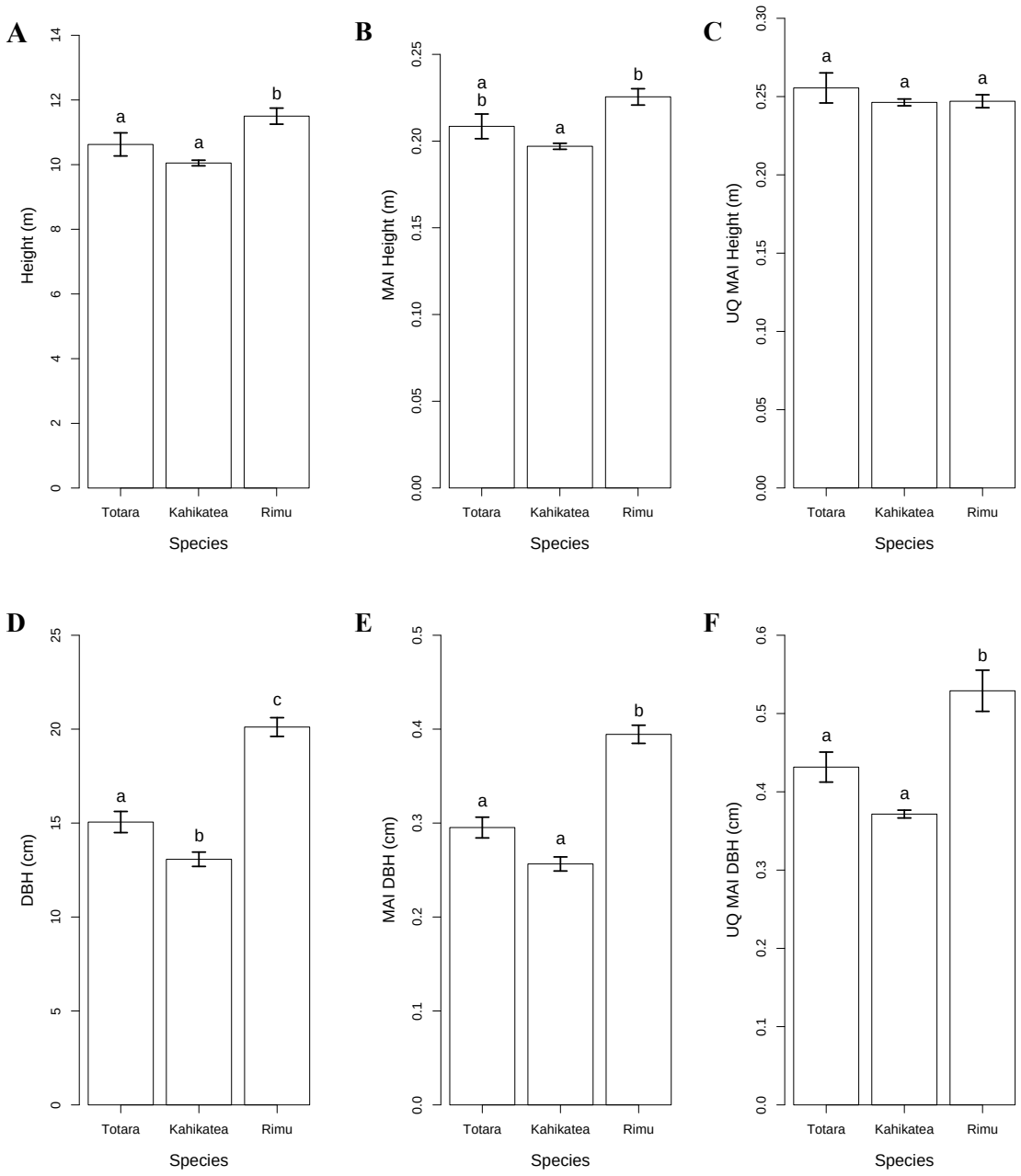


Figure 17. Mean height and diameter from stands of three podocarp species underplanted in a Ponderosa Pine plantation in New Zealand's central North Island.(A) Mean height, (B) MAI height, (C) UQ MAI height, (D) DBH, (E) MAI DBH, (F) UQ MAI DBH. Columns with coinciding letters indicate no significant difference, whereas columns with different letters indicate significant differences at $P < 0.05$. Error bars represent one standard error of the mean.

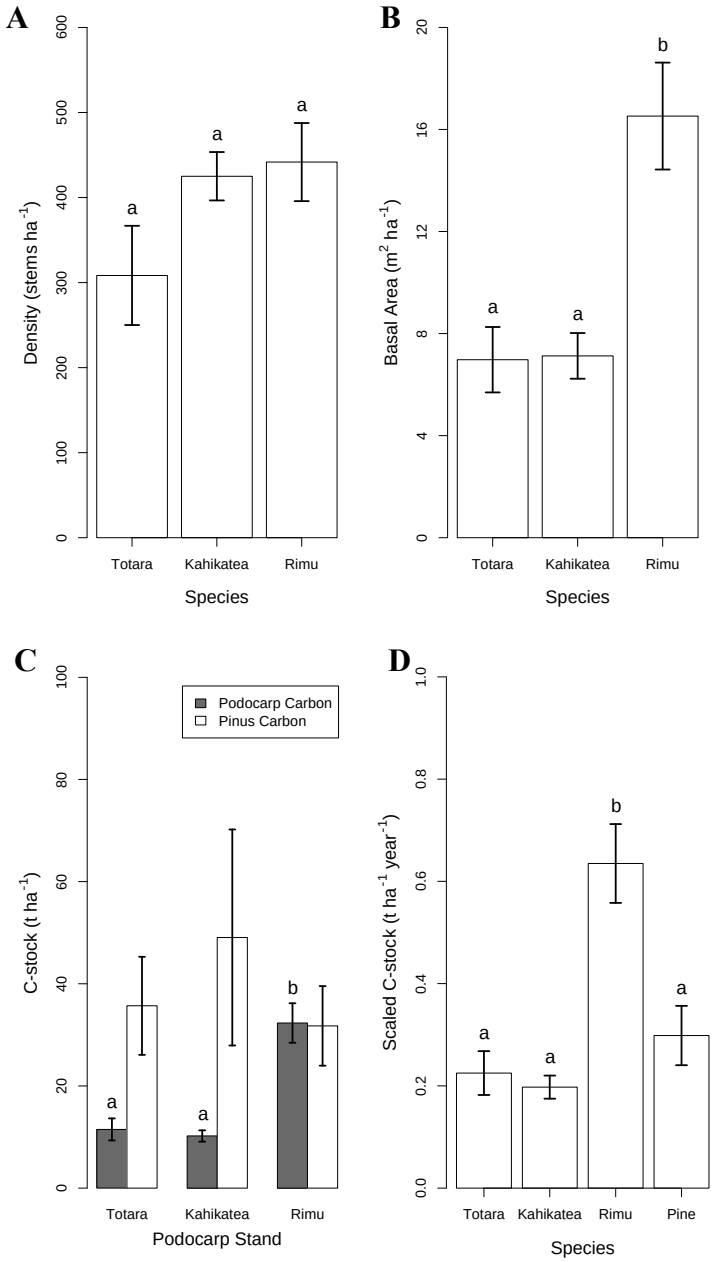


Figure 18. Mean density, basal area, and carbon stock results from stands of three podocarp species underplanted in a Ponderosa Pine plantation in New Zealand's central North Island.(A) mean stem density, (B) mean basal area, (C) mean C-stock of podocarp stands and Ponderosa Pine, (D) mean scaled C-stock (t ha^{-1}). Columns with coinciding letters indicate no significant difference, whereas columns with different letters indicate significant differences at $P < 0.05$. Error bars represent one standard error of the mean.

6.4.3. Forest Understorey Composition and Structure

A total of 30 vascular plant species were present within the understories of the three podocarp stands comprising 27 indigenous and three exotic species (Appendix I). A variety of life forms were present including 17 ferns, four shrubs, three trees, three lianes, one grass, one herb, and one sedge species. Understorey species richness (S) of each podocarp stand comprised mainly fern species (52–57% of total species richness across the three planted podocarp species). Potential future indigenous canopy dominants were present in the form of Kahikatea seedlings, found under both the Kahikatea and Rimu canopies, along with Rimu seedlings under the Rimu canopy only. A third tree species, the exotic Douglas-Fir (*Pseudotsuga menziesii*), was present in close association with Totara canopy cover. No Totara establishment was found.

Understorey composition differed significantly among stands ($F(2,9) = 7.35$, $P = < 0.001$), with Rimu composition being significantly different from Totara or Kahikatea (Fig. 20). Significant differences in indigenous species richness also occurred among different podocarp stands ($F(2,9) = 4.46$, $P = 0.045$). The Rimu stand (11.8 ± 1.49 S) supported the richest indigenous understorey composition, being significantly richer than the Totara stand (6 ± 0.40 S) (Fig. 21). Richness in the Kahikatea stand (9 ± 1.78 S) was intermediate between Totara and Rimu stands, but not significantly different from either. Total species richness was not significantly different among podocarp stands.

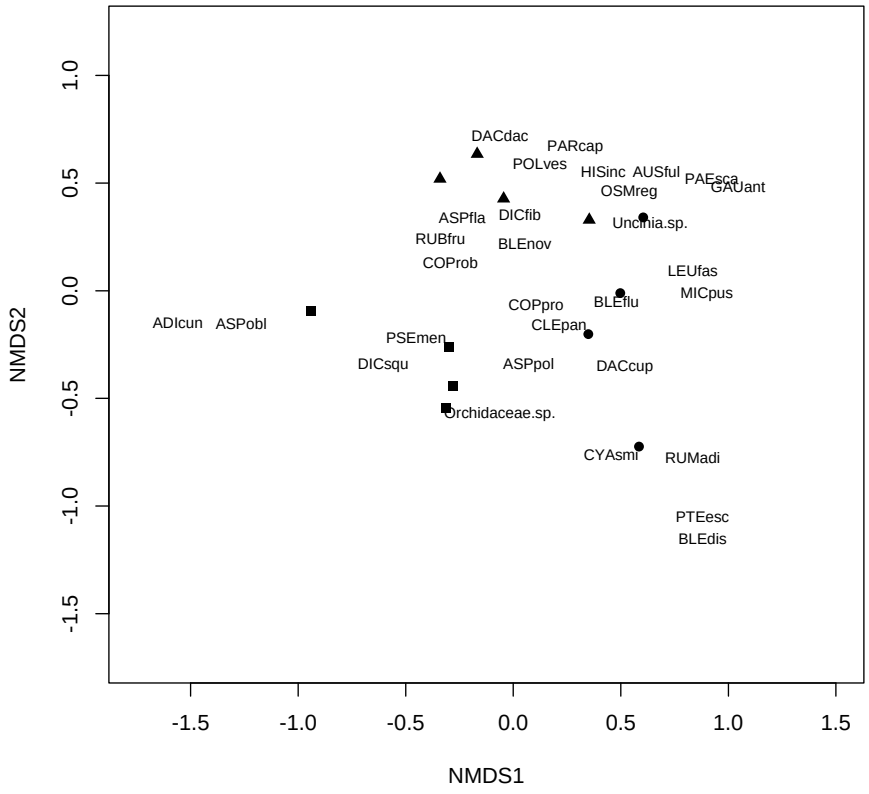


Figure 19. nMDS ordination of understorey species from stands of three podocarp species underplanted into a Ponderosa Pine plantation in New Zealand's central North Island. Totara = ■, Kahikatea = ●, Rimu = ▲. Species codes used are listed in Appendix I. Stress = 0.16.

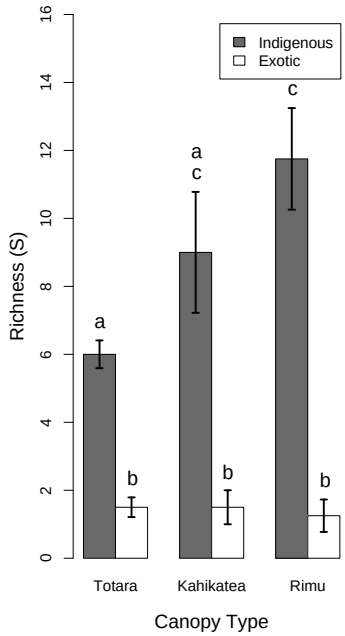


Figure 20. Indigenous vs. exotic flora species richness within the understories of three podocarp species underplanted in a Ponderosa Pine plantation in New Zealand's central North Island. Columns with coinciding letters indicate no significant difference, whereas columns with different letters indicate significant differences at $P < 0.05$. Error bars represent one standard error of the mean.

The most frequently occurring plant among the podocarp understories was Kiokio (*Blechnum novae-zelandiae*) which also had the greatest mean percentage cover of any species, 176% under Kahikatea (70.8% under Rimu, 8.6% under Totara) (Appendix I). Rough Tree Fern (*Dicksonia squarrosa*) showed high frequency and maximum percentage cover under Totara 125.4% (3.3% under Rimu, 3.1% under Kahikatea). Wheki-Ponga (*Dicksonia fibrosa*) showed a peak in frequency and cover (100%, 15.5%) under Kahikatea, with lesser frequency and cover under Rimu (75%, 6.8%). Karamu (*Coprosma robusta*), Prickly Shield Fern (*Polystichum vestitum*), New Zealand Jasmine (*Parsonsia capsularis*), and Blackberry (*Rubus fruticosus*) all showed maximum frequency and cover under Kahikatea. Rough Tree Fern discriminated most strongly between Totara and Kahikatea stands (20.05 ± 6.3% dissimilarity), and between Totara and Rimu stands (24.85 ± 7.4% dissimilarly) (Appendix J). The fern, Kiokio, had the greatest distinguishing influence on understorey composition between Kahikatea and Rimu stands (7.95 ± 4.7% dissimilarity) and between Kahikatea and Totara stands (13.48 ± 4.6% dissimilarity). Wheki-ponga discriminated Kahikatea from Totara (6.78 ± 3.3% dissimilarity), and Rimu from Totara (6.25 ± 4.2% dissimilarity).

6.5. DISCUSSION

6.5.1. Relative Podocarp Performance

The survey results support the hypotheses that an indigenous dominated forest structure is achievable within *ca.* 50 years through underplanting, and that Rimu would be the better performing of the three podocarp species. Underplanting the degraded pine plantation with three podocarp species has resulted in the development of podocarp stands that show clear differences in growth performance, with Rimu the best performer. Rimu has exceeded the declining 87-year-old Ponderosa Pine trees in terms of basal area, to be the most dominant tree. All three podocarp species have a greater stand density (stems ha^{-1}) than the contemporary Ponderosa Pine trees. However, all three podocarp species were still shorter than the Ponderosa Pine trees. These podocarp growth rates are less than published growth rates estimated for podocarps planted at lowland sites (Bergin & Kimberley, 2011; Pardy et al., 1992). This is likely because podocarp growth at upland sites is less than that possible for lowland sites (Bergin, 2000; Pardy et al., 1992).

Carbon storage within Rimu was significantly greater than in either Totara or Kahikatea. Per annum scaled C-stocks for Rimu were significantly larger than either of the

other podocarp species and also larger than the pine per annum C-stock. However, the Rimu stand is only in an early stage of development and the current Rimu C-stock (32.3 ± 3.87 t ha^{-1}) is considerably less than the estimated biomass carbon stocks for exotic plantation forest (88 t ha^{-1}) or mature podocarp forest (174 t ha^{-1}) (Ausseil et al., 2013). Rather, the Rimu C-stock is currently more comparable to the estimated carbon density of Manuka/Kanuka shrubland (51 t ha^{-1}).

We hypothesised that Rimu will have out performed both Totara and Kahikatea due to interspecific differences in light requirements, response to soil nutrient status, elevational distributions, and frost susceptibility. Totara and Kahikatea, both light demanding species, colonise recently disturbed sites and their seedlings have similar growth rates in high-light environments (Ebbett & Ogden, 1998; McKelvey, 1963; Cameron, 1960). Neither species grows well under a closed forest canopy (Bartlett, 1984; McSweeney, 1982), with Kahikatea seedlings growing best when > 40% of the sky was unobstructed (Bartlett, 1984). Totara regeneration is most vigorous in high-light environments such as large wind-throw gaps, forest margins, open scrub, and grassland. Totara regenerated well in Manuka/Kanuka (*Kunzea ericoides*) scrub, especially within canopy gaps (Bergin, 2000). Totara and Kahikatea are the most successful of all podocarp species to establish from nursery raised plants at open sites (New Zealand Forest Service [NZFS], 1980). In contrast, while small Rimu seedlings can show a good growth response in high-light conditions (McEwen, 1983), large seedlings have optimum growth in lower light conditions (Ebbett & Ogden, 1998; McEwen, 1983) and accordingly Rimu has been classed as a more shade tolerant species (Bartlett, 1984). Prior to 1975, planted podocarp seedlings had a pine cover of > 20–30% and the overhead shade provided by the degraded pine canopy would therefore benefit Rimu more than either Totara or Kahikatea.

The three podocarps differ in their growth response to nutrient availability. Kahikatea has a high ability to take up nutrients (Duncan, 1993) and Totara grows faster on more fertile sites (Norton et al., 1988). Totara and Kahikatea are known to have a similar growth response to differing levels of nutrient supply (Ebbett & Ogden, 1998), which suggests that factors other than nutrient supply are likely to drive distributional differences between Kahikatea and Totara (Hawkins & Sweet, 1989). Kahikatea is particularly competitive on flat, moist, nutrient rich mineral soils (Duncan, 1993; Hawkins & Sweet, 1989). Rimu is different, in that it has a high ability to uptake nitrogen and phosphorus at low rates of supply and is therefore

competitive on infertile sites (Hawkins & Sweet, 1989), such as the leached, relatively low nutrient, rhyolitic pumice tephra derived soils of the trial site.

Existing literature suggests that rimu should perform better at our upland site than the other two species. For example, our study site was at the upper end of the elevational range for Totara and Kahikatea, unlike Rimu (Bergin, 2000; Norton et al., 1988). A significant component of Rimu's wider elevational range is likely due to its superior frost tolerance. Totara and Kahikatea have been previously documented as relatively frost sensitive (Wardle, 1974; Beveridge et al., 1973) whereas Rimu has been shown to tolerate frosts to at least -8 °C (Sakai et al., 1981).

Underplanting has ensured the presence of podocarps as canopy dominants within the forest succession. Podocarps take a number of decades to enter natural successions, as observed by McKelvey (1955) and Cameron (1960). Approximately 30 km to the south-east of the trial site, McKelvey (1955) described a succession initiated by burning—colonised by *Pteridium esculentum,* to either broadleaved angiosperms, or Manuka or Kanuka, that would only then be invaded by podocarps. Podocarp colonisation was irregular and slow, dependent on dispersers, on pioneer shrub species to attract dispersers, and on good and regular podocarp seed years. Good stocks of podocarp seedlings would establish themselves 30–50 years on from burning, provided that a good seedling supply were available. At Whirinaki Forest, Cameron (1960) recorded podocarp establishment 40–60 years following clearance by burning.

Our results show that underplanting has ensured podocarps in the forest succession, and has removed the *ca.* 50-year time-lag (Cameron, 1960; McKelvey, 1955) associated with natural podocarp establishment.

6.5.2. Influence of Podocarps on the Forest Understorey

Embedded within exotic plantation forest, the trial site is isolated by a 12–13 km separation from natural indigenous forest. Despite some podocarp seedling establishment, we found no evidence of a woody forest succession developing from the plantation understorey. The almost exclusively indigenous understorey composition is comprised predominantly of fern species.

Underplanting is a particularly effective method of forest restoration in circumstances where the ability for natural dispersal is limited (Weber et al., 2011). Underplanting can ensure the presence of future forest canopy dominants that may not have arrived without intervention or may only have arrived at a later stage of forest development (Lamb et al., 2005). The artificial establishment of later-successional species also potentially accelerates the rate of successional development and directs successional development towards restoration objectives (Parker et al., 2001).

Dispersal limitation probably occurs at the trial site due to isolation from adjacent areas of indigenous forest and the absence of fruit and nectar sources to attract bird dispersers into the pine dominated landscape. Fruit and nectar sources attract the principal bird species that are responsible for dispersing indigenous forest tree seeds (Clout & Gaze, 1984). However, planting within the shelter of the degraded plantation understorey has been effective in artificially recruiting podocarps (especially Rimu), thereby overcoming the limitations on forest propagule dispersal.

Underplanting within the shelter of the degraded plantation has accelerated indigenous forest succession by introducing late-successional species and removing the *ca*. 50-year period associated with podocarp invasion of seral vegetation. The benefits of underplanting are found in the emerging structural dominance of podocarps (especially by Rimu) and in the relatively high indigenous fern species richness under the 51-year-old Rimu canopy.

Based on these results we propose that there is wider potential to use *Pinus* stands as sites for restoration of indigenous forest cover, either at non-harvest plantations, or perhaps amongst sparse naturalised stands (Norton & Forbes, 2013). Further research is required into management of *Pinus* stands as nurse crops within which later successional species can be recruited, thereby accelerating forest succession toward restoration goals.

6.6. CONCLUSIONS

Our results show that, with careful matching of underplanted species to environmental conditions, an indigenous dominated forest structure is certainly achievable within *ca.* 50 years of underplanting. Fifty-one years following planting, the best performing species, Rimu, has grown significantly faster than either Totara or Kahikatea and has obtained a stature in many regards similar to or better than the contemporary pine stand.

As a restoration strategy, underplanting degraded plantations is of particular value in circumstances where potential canopy dominants may be late to colonise, or where they do not have the ability to establish themselves naturally. Accelerated successional development can be achieved by underplanting late-successional, shade-tolerant, indigenous canopy dominants.

Correct species selection for underplanting is critical to the degree of restoration success, particularly with regard to the plantation understorey light environment and also to the site's environmental conditions. Selection of species can also have significant implications for the understorey that assembles within the underplanted forest. However, the isolated nature of the study site has limited subsequent successional development.

7. CHAPTER SIX:

Synthesis

CHAPTER PREFACE

The first objective of this thesis is to examine the potential long-term role of non-harvest *P. radiata* plantations as a means of restoring indigenous forest cover in New Zealand. The second objective of this thesis is to gain an understanding of the ecological processes that act to constrain indigenous forest regeneration patterns in New Zealand exotic conifer non-harvest plantations. From the understanding gained of the processes that might constrain indigenous forest regeneration, the third thesis objective is to describe interventions that can be used to optimise forest regeneration processes.

Chapter Six synthesises and concludes on the preceding chapters, in the context of the thesis objectives.

7.1. RESTORATION POTENTIAL OF NON-HARVEST *P. RADIATA* STANDS

7.1.1. Patterns and Processes Relevant to Long-Term Regeneration

This research shows that, despite its exotic identity, planted *P. radiata* can fill the role of a nurse species, one that facilitates the initiation of indigenous forest regeneration. This process occurs because the planted *P. radiata* trees grow rapidly, and canopy closure ameliorates climatic conditions. The *Pinus* stand facilitates a regeneration trajectory characterised by an increasingly species-rich, shade-tolerant, and longer-lived assemblage of indigenous forest species. The successional direction observed is consistent with the acquisition of traits associated with later-successional species, namely: larger seeds, greater stature, and greater longevity (Weiher et al., 1999).

The chronosequence survey extended to 89 years and is the longest duration survey of *P. radiata* understorey regeneration carried out in New Zealand to date. The findings of this survey confirm and build upon the existing evidence on the importance of stand age as a predictor of indigenous woody species richness. Existing literature from both New Zealand (Brockerhoff et al., 2003; Ogden et al., 1997; Allen et al., 1995) and overseas (Senbeta et al., 2002; Keenan et al., 1997) demonstrates the importance of plantation stand age for understorey regeneration – here, we find that both older stands and a proximal seed source of later-successional indigenous species are required for optimal facilitation of indigenous forest regeneration. The surveys of canopy openness and total PAR transmission show that, after 15 years, average canopy openness and total PAR transmission will each have been reduced by approximately two-thirds, to levels of about 30% each. This period from establishment to about 15-years is characterised first by an invasion, then accumulation, and finally decline of light-demanding, colonising species. After this time, species of increasing shade-tolerance accumulate. This observed pattern of initial turnover of light-demanding colonisers followed by the accumulation of an increasingly shade-tolerant understorey is consistent with the findings of previous surveys of understorey regeneration within exotic plantation forests (Brockerhoff et al., 2003; Hill, 1979).

The presence of mature forest canopy species in the stand closest to indigenous forest, is to a degree contrary to earlier research findings (Allen et al., 1995; McQueen, 1993) that tall-forest or old-growth canopy species are unable to inhabit *P. radiata* plantations, and that

this floristic inequality sets *P. radiata* plantations apart from indigenous forest communities. However, the presence of mature forest canopy species in a mature *P. radiata* plantation is supported by the findings of Brockerhoff et al. (2003), who also recorded *B. tawa*, and the indigenous forest canopy species *E. dentatus* and *P. ferruginea* inhabiting mature *P. radiata* stands.

This research demonstrates that proximity to indigenous forest is important for forest regeneration in mature stands—where age-related structural development has moderated microclimate conditions, and where propagules are available from proximal indigenous forest then have suitable conditions to establish themselves. While the importance of proximity to indigenous forest has been suggested in previous surveys of *P. radiata* plantation understorey composition (Brockerhoff et al., 2003; Allen et al., 1995), this research appears to be the first New Zealand work to present specific data on the effect of indigenous forest proximity on indigenous woody species richness in exotic *P. radiata* plantations. Although, as only one stand in each age class was available for inclusion in our chronosequence design, we are unable to generalise from our results regarding the importance of indigenous forest proximity for regeneration processes in *P. radiata* plantations. Rather, we propose proximity is an important predictor of indigenous regeneration patterns and recommend this aspect is worthy of further research. Nevertheless, our finding regarding indigenous forest proximity is consistent with international studies that demonstrate the critical role of proximity of indigenous forest seed sources (Onaindia & Mitxelena, 2009; Lee et al., 2005; Senbeta et al., 2002; Chapman & Chapman, 1996).

While a suite of generalist indigenous forest flora is able to inhabit ecologically isolated *P. radiata* stands, the limitations on the establishment of species that produce large seeds infrequently and which require bird dispersers are a key implication for restoration management of isolated non-harvest *P. radiata* plantations. This finding highlights the importance of retaining indigenous cover in a landscape matrix (Lindenmayer & Hobbs, 2004; Craig et al., 2000), the benefits of which extend beyond the boundaries of indigenous sites, where they are expressed in the structure and composition of adjacent exotic planted forests. Further research is required to better understand how different configurations of indigenous forest proximity (the combination of separation distance and extent) influence indigenous forest regeneration in exotic *P. radiata* plantations. Also, as indigenous vegetation communities differ in their composition, research to understand the importance of proximity

to specific resources for frugivores and nectivors for *P. radiata* understorey regeneration is necessary.

7.1.2. Non-Harvest *P. radiata* Stands as Restoration Sites in New Zealand's Highly Modified Lowland Landscape

In evaluating the potential role of non-harvest *P. radiata* plantations as indigenous forest restoration sites, it is beneficial to consider my research results in the context of New Zealand's highly modified lowland landscape.

The Roles of Ecological Isolation and Disturbance

Most of New Zealand's contemporary lowland forests are of a fragmented configuration (Norton & Miller, 2000). Representative floral components of these lowland forests, such as podocarps or angiosperm mature forest canopy species, are often either scarce or are absent. Where this occurs, the important role that these forest components play in providing a source of propagules is also lost, and processes such as dispersal and recruitment of long-lived mature forest canopy species are impaired, or might even become effectively extinct at a local scale (Craig et al., 2000).

Inevitably, the absence of propagule sources has implications for the composition of future forests (Sullivan et al., 2007; Duncan & Chapman, 1999). While my chronosequence survey found an increasingly species-rich, shade-tolerant, and longer-lived assemblage of indigenous forest species – my results also confirm that ecological isolation from indigenous forest seed sources is a key factor constraining a successional trajectory towards an old-growth indigenous forest composition. This is consistent with the wider pattern in today's modified lowland landscape, where the limitations on dispersal of mature forest canopy species into both indigenous (Coomes et al., 2003) and exotic (Sullivan et al., 2007) forest communities affect the successional trajectory and the future forest composition. Therefore, the problem that I identify, of the limited dispersal of mature forest canopy species into non-harvest *P. radiata* stands, is a broader contemporary issue and is relevant to secondary forest successions in both indigenous and various exotic forest communities.

I found an absence of podocarps across the *P. radiata* chronosequence, but this has also been observed in natural forests. Podocarp regeneration has been the subject of specific research for some time in New Zealand (Lusk et al., 2009; Lusk & Ogden, 1992; Wardle,

1963). Podocarps are known to have specific disturbance related requirements for establishment (McKelvey, 1952), and a resultant naturally discontinuous age structure (Lusk & Ogden, 1992). In contrast, broadleaved angiosperms are known to be faster growing (Coomes et al., 2005) and tend to have continuous regeneration and age structure (Lusk et al., 2009). The contemporary lowland landscape of the Kinleith Forest study area features a scarcity of podocarp seed sources. Commercial plantations are generally < 30-years-old – meaning most stands are probably too young to expect podocarps to establish themselves. Even non-harvest *P. radiata* stands may be managed to minimise disturbance (e.g., wildfire) which would mean, without interventions such as canopy gap creation, these stands would not receive the disturbance that is a characteristic requirement for significant podocarp regeneration. In contrast, broadleaved angiosperms are more common and therefore seed sources are comparatively more abundant. Broadleaved species do not share the podocarps' strong dependency on disturbance for regeneration. Considering the specific requirements for podocarp establishment, and the scarcity of podocarp seed sources in the contemporary landscape, it is not surprising that podocarps were not found in my *Pinus* chronosequence survey.

Alternative Successional Trajectories in New Zealand's Exotic Forests

In place of former indigenous forest, the contemporary New Zealand landscape contains both monocultures and mixed-exotic forests, many of which have the potential to facilitate indigenous forest regeneration (Williams, 2011). While *P. radiata* plantations provide one example of these common exotic forest types, other examples include forests of *Ulex europaeus* (gorse; Fabaceae), *Salix* spp. (willow spp.; Salicaceae), *Acer pseudoplatanus* (sycamore; Sapindaceae), and *Sambucus nigra* (elder; Caprifoliaceae). Where forest regeneration occurs within the understoreys of these forests, specific canopy types lead to different patterns in both understorey composition and the successional trajectory that might ensue. For example, successions through the exotic *U. europaeus* and indigenous *Kunzea* follow different successional pathways, and lead to different forest types (Sullivan et al., 2007; Williams & Karl, 2002). Comparative studies of *U. europaeus* and *Kunzea* have shown that stands of each support a different composition of species, and that *U. europaeus* has a lower species richness compared to *Kunzea* (Williams & Karl, 2002; Allen et al., 1992; Lee et al., 1986). Stands of *Salix* (Pratt, 1999; Wardle, 1991) and *A. pseudoplatanus* (Williams, 2011) have been observed or predicted (Meurk & Hall, 2006) to facilitate the recruitment of

both broadleaved angiosperms and podocarps, although based on existing knowledge, the successional trajectory of these two exotic forest types towards indigenous dominance is uncertain (Williams, 2011; Meurk & Hall, 2006). The above then suggests that secondary successions from naturalised vegetation communities will not always be of a similar composition to indigenous successions (Williams, 2011).

Factors explaining differences in successional trajectory and future forest composition include: The initial indigenous to non-indigenous ratio, the longevity of the exotic nurse stand, and differences in stand structure (Williams, 2011). For plantation *P. radiata* the preceding clear-fell and site preparation operations mean that the planted *Pinus* are a monoculture. In order for any indigenous forest canopy dominants to form part of the future forest, those canopy dominants must establish themselves. The longevity of plantation *P. radiata* stands in New Zealand conditions is unknown, and further research is required to understand the dynamics of the recruitment of mature forest canopy species from *P. radiata* understoreys and their attainment of canopy dominance. The nursery role of *P. radiata* plantations has been compared to that of the indigenous *Kunzea* (Meurk & Hall, 2006; Brockerhoff et al., 2003). Existing predictions of the transition from *P. radiata* forest to forest dominated by indigenous canopy species suggests that, with interventions such as a continuous-canopy thinning regime, *P. radiata* would be replaced by mature forest canopy species in about 200 years (Meurk & Hall, 2006). This 200-year period is a similar transitional duration to that observed in natural *Kunzea* stands (Meurk & Hall, 2006).

My research shows that the successional trajectory and future forest composition would be strongly dependent on either the proximity of indigenous forest or on interventions to introduce mature forest canopy species where they are unable to establish themselves. Some questions remain as to the degree of similarity of the successional trajectory with that through indigenous seral species. Further, it was observed that proximal indigenous seed sources (forest remnants) play a critical role in the establishment of later-successional species. Together, these observations suggest that the successions would benefit from further management at selected stages of the succession.

Goals for Forest Succession using Non-Harvest P. radiata

This research shows that where *P. radiata* plantations are managed on a non-harvest basis, these forest stands represent sites with sheltered conditions, long-term stability and an

associated potential for the recruitment of later-successional indigenous forest canopy species. This is a particularly important opportunity for restoration of indigenous forest cover in commercially-productive lowland landscapes where the options for restoration of indigenous forest cover are often limited by the repetitive disturbances associated with productive land use practices.

My results show that in New Zealand's contemporary lowland environments, where commercially productive land uses prevail, the realistic goals for a secondary forest succession in non-harvest *P. radiata* stands are dependent on the stand's age, the stand's proximity to indigenous forest remnants, and the degree to which management interventions are undertaken to accelerate and direct understorey regeneration.

In non-harvest *P. radiata* stands located in close proximity to indigenous forest seed sources it is realistic to expect the occurrence of late-successional broadleaved species and a long-term successional trajectory with similarities to mature indigenous forests of the area (Brockerhoff et al., 2003; Ogden et al., 1997; Allen et al., 1995). Podocarps would only be expected to occur in low densities, or otherwise would be absent. Control of mammalian browsers should be considered in order to promote the recruitment of palatable indigenous mature forest canopy species (Forsyth et al., 2002). The interventions discussed below might still be valuable methods of accelerating and directed successional development.

At sites that are ecologically isolated due to a large separation distance from areas of indigenous forest remnants (seed sources), my results show that it is realistic to expect to achieve an independent forest canopy comprising generalist shade-tolerant indigenous tree species. In the Kinleith Forest study area, this generalist forest tree composition included species such as *B. repanda*, *P. arboreus*, *P. tenuifolium*, *S. digitata*, *M. australis*, and *M. ramiflorus*. Additional species, perhaps including longer-lived canopy dominants might appear but this would only occur from infrequent long-distance dispersal (Wootton & Kelly, 2012), and therefore this would be an insignificant component of the composition. To achieve a greater density of generalist forest trees, a greater woody species richness, or to direct successional development toward old-growth natural forest composition, management interventions are likely to be required and control of mammalian browsers should be considered in order to promote the recruitment of palatable indigenous mature forest canopy species (Forsyth et al., 2002).

7.1.3. Accelerating and Directing Understorey Regeneration

While non-harvest *P. radiata* plantations present potential sites for the regeneration and recruitment of indigenous forest flora, this research has found a number of factors that influence the structural or compositional aspects of understorey regeneration and that potentially could be modified to speed up the successional process.

Artificial canopy gap creation to reduce canopy shading

This research is the first to examine the effect of canopy gap interventions on the growth rates of mature forest canopy species in New Zealand's exotic *P. radiata* plantations. The creation of small-scale artificial canopy gaps within an 18-year-old *P. radiata* plantation provided a means of significantly increasing light transmission to the forest understorey. The results show that small-scale artificial canopy gaps can be used to optimise understorey illumination and thereby to accelerate the growth of mature indigenous forest canopy species. The results also show that canopy gap size has important implications for growth performance of different mature forest canopy species, according to the respective species shade-tolerance related life history traits. The light-demanding *P. totara* grew at a significantly greater rate in large canopy gaps (5.6 m radius; 0.58 gap ratio; 84% of total available light transmitted), whereas the shade-tolerant *B. tawa* grew most consistently in small canopy gaps (2.3 m radius; 0.40 gap ratio; 50% of total available light transmitted). The occurrence of browse by introduced mammals increased with canopy gap creation. This then suggests that where canopy gaps are created, management should also consider methods to mitigate the effects of browsing mammals, such as the selection of species of low palatability, high density plantings, the use of felled trees as forest slash barriers to act as physical protective barriers around seedlings (Rumble et al., 1996), or the active management of the mammalian populations.

Without intervention, the plantation *P. radiata* canopy constitutes an even-aged monoculture of homogenous structure, particularly in younger stands once canopy closure has been achieved. Canopy heterogeneity is an important consideration for restoration in non-harvest plantations, as low structural diversity might limit understorey plant species richness (Gamfeldt et al., 2013), the recruitment of future canopy species on the site (Royo & Carson, 2006), or the development of wider biodiversity values. Forest canopy gaps play a critical role in influencing the understorey light regime (Canham et al., 1990), and the natural

development of structural heterogeneity, such as canopy gaps, is likely to take an extended period of time to occur without intervention (Kuuluvainen et al., 2002). Canopy opening, whether artificially created or though natural processes, would also be required to physically allow the recruited indigenous trees to occupy space in the canopy tier. The process of long-term senescence and mortality in New Zealand *P. radiata* plantations has not been systematically studied and, therefore, no data are available to anticipate how the structural changes of the declining *P. radiata* plantation would allow for the recruitment of indigenous canopy tree species to the forest canopy. Nor is it known what the typical lifespans for *P. radiata* trees are for New Zealand conditions, or what the implications are of the physical disturbance effect from the eventual toppling of dead *Pinus* trees for understorey regeneration processes, especially given the relatively high density and large biomass of the mature *P. radiata* plantations.

The creation of artificial canopy gaps has also proven to be a successful forest restoration technique in Canadian *P. resinosa* (Parker et al., 2001) and Sri Lankan *P. caribaea* (Ashton et al., 1997) plantations. My research provides evidence for the role of artificial canopy gap creation in New Zealand *P. radiata* plantations as a means of increasing heterogeneity in the planted forest, and optimising these exotic plantations for the growth of mature indigenous forest canopy species.

Understorey manipulation to accelerate woody seedling growth

This research has been the first to examine the competitive effects of dense tree fern stands on seedling growth rates of mature indigenous forest canopy trees in New Zealand's exotic *P. radiata* plantation forests. The interception of light by dense understorey vegetation can critically influence forest regeneration and the rate and direction of successional development (Royo & Carson, 2006; George & Bazzaz, 1999; Bazzaz & Pickett, 1980). Therefore, the development of dense understorey vegetation in non-harvest plantation forests is of particular interest where those forests are managed for the restoration of indigenous forest cover.

The competitive shading effect by dense tree fern stands has been identified both in New Zealand's temperate podocarp-broadleaved forest (Gaxiola et al., 2008; Carswell et al., 2007; Coomes et al., 2005) and internationally in other naturally occurring vegetation communities (Walker et al., 2010; Mueller-Dombois, 2000). As tree fern dominated

understories are also known to develop in New Zealand's central North Island *P. radiata* plantations (Ogden et al., 1997; Allen et al., 1995), the competitive effect of these dense tree fern stands on seedling growth rates of mature forest canopy species is relevant where non-harvest *P. radiata* stands are to be managed for the restoration of indigenous forest cover.

The results of the tree fern competition experiment show that the tree fern community was dominated by one species, *Dicksonia squarrosa*, and that tree fern stands reached total densities of 2153±260 stems ha^{-1}. This density is similar to those measured from nearby central North Island *P. radiata* plantations by Ogden et al. (1997). The heavy shade cast by tree ferns significantly reduced the growth rates of two mature forest canopy species: *Pittosporum eugenioides* and *Podocarpus totara*. Browsing by introduced mammals was also increased with the removal of tree fern cover. The species life history traits regarding growth rates and tolerance of shade were important in explaining the absolute growth benefits from tree fern removal. The seral *P. eugenioides* achieved greater growth compared to the slower growing and comparatively less light-demanding, *P. totara*. The occurrence of animal browse was also important for the growth benefits achieved from tree fern removal. Even when the browsed seedlings of *P. eugenioides* were taken into account, tree fern removal in the presence of browsers resulted in significantly greater height growth rates compared to those *P. eugenioides* seedlings growing amongst dense tree fern stands. In contrast, the slower growing *P. totara* was less competitive in the presence of browsers, and the species did not achieve significantly greater growth rates where tree ferns were removed in the presence of browsers.

These results demonstrate that dense tree fern stands have the potential to significantly limit the seedling growth rates of mature indigenous forest canopy species growing in mature *P. radiata* plantations. This finding is consistent with the heavy shading effect that tree ferns have been found to have on the forest floor environments of natural forests (Bystriakova et al., 2011; Gaxiola et al., 2008; Coomes et al., 2005). Where non-harvest *P. radiata* stands are managed for the restoration of indigenous forest cover, thinning interventions to reduce the competitive effects of dense tree ferns stands may be necessary. The choice of species according to growth rates, shade tolerance, and palatability is a critical consideration if introducing mature forest canopy species into these exotic plantation forests, and the management of introduced mammalian browser populations would likely be beneficial for maximising seedling height growth rates.

Similarly, the results from the survey of indigenous woody epiphyte establishment on tree fern trunks demonstrated a significant negative association between tree fern stand density and the number of woody epiphytes found on tree fern trunks. In the context of interventions to address tree fern dominance, this negative association suggests that retaining mature tree ferns at low densities, where shading from tree ferns is reduced, is a means of providing additional opportunities (i.e., epiphytic substrates) for seedling establishment in these exotic plantation forests. Therefore, from a management perspective, the ideal is to find a balance between having too many tree ferns that limit indigenous vegetation establishment while still retaining enough tree ferns to act as establishment sites for epiphytically establishing indigenous canopy tree species.

Underplanting to accelerate and direct succession

This research assessed the largest known forest underplanting trial carried out in New Zealand, which is also one of the few underplanted trials carried out within a non-harvest *Pinus* plantation. The underplanting survey represented 50 years of forest development since the New Zealand Forest Research Institute (FRI) established about 24 000 nursery-raised seedlings of the native conifer species *Podocarpus totara*, *Dacrycarpus dacrydioides*, and *Dacrydium cupressinum* within a degraded *P. ponderosa* plantation located in Kaingaroa Forest, in New Zealand's central North Island.

Underplanting is a technique that has been used internationally to incorporate mature forest canopy species into *Pinus* plantations (Knapp et al., 2013; Noack, 2011; Rodriguez-Calcerrada et al., 2008; Ashton et al., 2001; Parker et al. 2001; Gilmore, 2000). Underplanting is a particularly useful means of incorporating larger-seeded species that are dependent on birds for dispersal, and that therefore may take a long time to establish themselves or that may never establish themselves naturally at a site (Weber et al., 2011; Lamb et al., 2005). Thus, underplanting is a means of addressing the dispersal limitation issue identified in the chronosequence study. Underplanting also provides a means of incorporating specific species in order to direct and accelerate successional development towards restoration objectives (Parker et al., 2001). The chronosequence survey demonstrates that the woody indigenous floral composition of *P. radiata* plantations is influenced by proximity to indigenous forest, and this FRI underplanting trial site is located *ca*. 12–13 km from tracts of indigenous forest cover and, therefore, can reasonably be considered ecologically isolated in the context of dispersal of forest propagules.

Fifty-years on, the survey results show that underplanting of the degraded non-harvest *Pinus* plantation with mature forest canopy species is a means of accelerating and directing the composition and structure of understorey regeneration patterns. However, considerations over the choice of species are important, as was demonstrated in the underplanting survey results, where *D. cupressinum* significantly outperformed both *D. dacrydioides* and *P. totara*. Differences in performance can be found in the respective species' differing tolerance of shade, as well as other interspecific biotic and abiotic preferences. Within the shelter of the degraded *P. ponderosa* stand, the shade tolerant *D. cupressinum* achieved significantly greater basal area (16.5±2 m^2 ha^{-1}) and height (11.5±0.25 m), compared to either of the more light-demanding species, *D. dacrydioides* and *P. totara.* After 50 years, *D. cupressinum* had exceeded the declining 87-year-old *P. ponderosa* plantation in terms of basal area, to become the most dominant tree species at the trial site. Importantly, this research has also found that underplanting achieved more than just the successful establishment of a stand of mature forest canopy species within a degraded *Pinus* plantation. The understorey compositions among planted species were significantly different, whereby *D. cupressinum* supported a significantly greater richness of indigenous flora compared to either *D. dacrydioides* or *P. totara.* However, the isolation of this site from native seed sources did limit the species that were establishing themselves in the developing indigenous understorey.

These results contribute to the existing literature on the potential of underplanting *Pinus* plantations with mature forest canopy species as a means of directing and accelerating successional development, particularly at ecologically isolated sites where large-fruited species that are dependent on birds for dispersal might not be able to establish themselves. Although all three species were establishing themselves and growing well, in terms of maximising restoration outcomes, the differing performance among species illustrates the importance of choosing species suited to both the understorey light conditions, and to other biotic and abiotic factors that might also act to influence growth performance. In addition to the obvious benefits of establishing stands of mature forest canopy species, the results show that the microclimate conditions created, over time, by the planted trees also have the potential to influence the outcome of the restoration of indigenous flora and indigenous biodiversity. The differences in performance among the three planted species are also supported to a degree by the results of both the artificial canopy gap creation and tree fern thinning experiments: That those results demonstrate how vegetation structure modifies the

quality and quantity of light available, and how species perform differently in those modified conditions according to their shade-tolerance and growth-rate related life history traits.

7.1.4. Implications for Plantation Owners

Pinus radiata plantations can be held under a non-harvest management regime for a variety of social, economic or environmental reasons. However, the potential opportunities from non-harvest *P. radiata* forests for plantation owners have received only limited attention in New Zealand. While this research primarily focuses on non-harvest *P. radiata* stands as sites for the restoration of indigenous forest cover, it is worth noting that the development of indigenous forest communities might lead to benefits and services additional to biodiversity, such as carbon storage by mature canopy trees that are recruited within the non-harvest stand. Evidence of the potential for this is found in the results of the underplanting trial. Therefore, forest managers might adopt multiple non-harvest objectives, such as restoring indigenous forest cover, and sequestering carbon.

An example is provided by central Government's Permanent Forest Sink Initiative (PFSI; Ministry of Primary Industries [MPI], 2015), where private landowners legally protect their forest by covenant with the Crown and manage the forest under a continuous-cover regime, to establish a permanent forest with uneven age structure. Landowners then receive carbon units in return. Under the PFSI, continuous-cover harvesting allows no more than 20% basal area ha^{-1} to be removed, and this harvesting is suggested to entail the removal of only single trees or small groups of trees (MPI, 2015). The results from the underplanting trial show that with careful selection of species, it is possible within 50 years to recruit a stand of mature forest canopy species within a *Pinus* stand. The results from the artificial canopy gap experiment show that the creation of small-scale canopy gaps, such as those that might be created from continuous-cover forest harvest, could potentially be used to optimise understorey illumination for the growth of indigenous tree species. Following this approach, the objective could be to transition the exotic *Pinus* stand towards indigenous dominance, by underplanting with suitable mature forest canopy species, while maintaining continuous forest cover. In the context of carbon storage, this transition would then present the opportunity for the initial and rapid carbon uptake by the fast growing planted *Pinus*, followed by the transitioning to mature forest canopy species with greater wood density and tree longevity, which would then potentially store more carbon over much longer time periods compared to *Pinus* (Chazdon, 2008).

The implications of this research are also relevant to commercial plantation owners when stands are retired from the commercial harvest regime and could contribute towards "reserve" requirements under certification systems such as the Forest Stewardship Council and could also be used to improve values in remnant indigenous forest areas through buffering and improving connectivity. Non-harvest areas within the plantation matrix present the opportunity for long-term forest development. Stands can be prioritised in favour of proximity to indigenous forest remnants in order to maximise natural dispersal. Incorporating and managing indigenous forest cover within the exotic plantation matrix is a method of enhancing indigenous biodiversity in plantation forests (Norton, 1998), even where plantations are managed under a clear-fell harvest regime. One method of using non-harvest stands to incorporate indigenous forest cover into the exotic plantation matrix, and between forest harvest rotations, would be for forest owners to recognise a mosaic of non-harvest stands—to achieve a recognised network of "non-harvest plantation reserves". This could be especially valuable as a tool to buffer or expand existing high value native forest remnants within plantations, or as a method to enhance connectivity between remnants.

This research shows that management interventions are a means of aiding the restoration of indigenous forest cover in non-harvest stands. These interventions include canopy opening, thinning of dense understorey vegetation, and enrichment interventions such as underplanting ecologically isolated sites, or at sites where the transition to indigenous forest is desired. In this sense, non-harvest *P. radiata* stands can be "engineered" to maximise their value as forest restoration sites. Therefore, these treatments are potential tools for commercial foresters where non-harvest sites exist and where there is a desire to promote the regeneration of indigenous forest cover within the plantation matrix. In a similar vein, plantations are known for their role in buffering indigenous communities and enhancing connectivity across managed landscapes (Brockerhoff et al., 2008a; Carnus et al., 2006). The longevity and forest development associated with non-harvest stands potentially heighten their buffing and connectivity values, particularly where non-harvest stands are located in close proximity to indigenous forest cover, or when interventions are taken to enhance indigenous regeneration in non-harvest plantation stands.

7.2. FUTURE RESEARCH

This research highlights the following points for future research:

1. Investigation into policy changes to MPI's Permanent Forest Sink Initiative (MPI, 2015), to allow for a managed progression from exotic to indigenous forest dominance whilst retaining or enhancing carbon storage.

2. Examination of the likely canopy dynamics associated with the long-term transition from *Pinus* plantation canopy towards indigenous dominance. This might involve canopy dynamics modelling to derive predicted management requirements to facilitate the switch to indigenous dominance.

3. Production of practical forest restoration guidelines for New Zealand plantation owners who wish to transition their exotic *P. radiata* plantation to indigenous forest. This might be required to support Point 1, and might be partly informed by Point 2.

4. Further research into the effect that differing degrees of indigenous forest proximity (the combination of separation distance and extent) have on regeneration patterns in *P. radiata* understories.

5. Further research into the effect that proximity of *P. radiata* plantations to specific resources for frugivores and nectivors has on patterns of regeneration in *P. radiata* understories.

6. A quantitative comparison of regeneration and the successional trajectory between *P. radiata* plantation forest and indigenous seral species.

7. Investigation into the views of commercial plantation owners, and quantification of the pros and cons, of establishing "non-harvest reserve networks" amongst commercial plantations estates.

8. Logistical and economic evaluation of timber harvest from small-scale canopy gap creation, in particular, to determine the following: Whether continuous-cover harvest to create small-scale canopy gaps would provide a revenue source sufficient to support restoration costs, or for example, whether felled trees are

better retained to increase habitat heterogeneity and to provide physical protective barriers for forest regeneration.

9. Further research into the potential for incorporating multiple species of varying shade tolerance within small-scale artificial canopy gaps based on spatial variation in gap-microclimate.

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9. APPENDICES

9.1. APPENDIX A: CHRONOSEQUENCE SPECIES LIST

Table 9. Woody species found in Kinleith Forest *Pinus radiata* plantation chronosequence (including indigenous reference site), central North Island, New Zealand

Species	Code	Family	Growth Form
Aristotelia serrata	ARIser	Elaeocarpaceae	Tree
Beilschmiedia tawa	BEItaw	Lauraceae	Tree
Brachyglottis repanda	BRArep	Compositae	Tree
*Buddleja davidii**	BUDdav	Scrophulariaceae	Shrub
Coprosma australis	COPaus	Rubiaceae	Tree
Coprosma robusta	COProb	Rubiaceae	Tree
Coriaria arborea	CORarb	Coriariaceae	Tree
Cordyline banksii	CORban	Asparagaceae	Tree
Cotoneaster sp.*	COTsp.	Rosaceae	Shrub
Cyathea dealbata	CYAdea	Cyatheaceae	Tree fern
Cyathea medullaris	CYAmed	Cyatheaceae	Tree fern
Dacrydium cupressinum^	DACcup	Podocarpaceae	Tree
Dicksonia squarrosa	DICsqu	Dicksoniaceae	Tree fern
Dicksonia fibrosa	DICfib	Dicksoniaceae	Tree fern
Cyathea smithii	DICsmi	Cyatheaceae	Tree fern
Fuchsia excorticata	FUCexc	Onagraceae	Tree
Gaultheria antipoda	GAUant	Ericaceae	Shrub
Geniostoma ligustrifolium	GENlig	Loganiaceae	Shrub
Hedycarya arborea	HEDarb	Monimiaceae	Tree
Knightia excelsa	KNIexc	Proteaceae	Tree
Leucopogon fasciculatus	LEUfas	Ericaceae	Shrub

Species	Code	Family	Growth Form
*Leycesteria formosa**	LEYfor	Caprifoliaceae	Shrub
Litsea calicaris	LITcal	Lauraceae	Tree
Melicytus ramiflorus	MELram	Violaceae	Tree
Myrsine australis^	MYRaus	Primulaceae	Tree
*Pinus radiata**	PINrad	Pinaceae	Tree
Pittosporum eugenioides^	PITeug	Pittosporaceae	Tree
Pittosporum tenuifolium	PITten	Pittosporaceae	Tree
Podocarpus totara^	PODtot	Podocarpaceae	Tree
Pomaderris amoena	POMamo	Rhamnaceae	Shrub
Prumnopitys ferruginea^	PRUfer	Podocarpaceae	Tree
Prumnopitys taxifolia^	PRUtax	Podocarpaceae	Tree
Pseudopanax arboreus	PSEarb	Araliaceae	Tree
Pseudopanax crassifolius^	PSEcra	Araliaceae	Tree
Pseudowintera colorata^	PSEcol	Winteraceae	Tree
Schefflera digitata	SCHdig	Araliaceae	Tree
Weinmannia racemosa	WEIrac	Cunoniaceae	Tree

Note. * = exotic flora. ^ = species found only in the mature natural forest reference site.

9.2. APPENDIX B: FORBES ET AL. 2015 RESTOR. ECOL.

Forbes, A. S., Norton, D. A. and Carswell, F. E. (2015) Artificial canopy gaps accelerate restoration within an exotic *Pinus radiata* plantation. Restoration Ecology. doi: 10.1111/rec.12313

9.3. APPENDIX C: CANOPY GAP PLOT CHARACTERISTICS

Table 10. Experimental plot site characteristics

Ref.	Treatment	Slope (◦)	Aspect (◦)	Topo. Unit (%)
1	Control	30	010	28.9
2	Control	33	350	28.0
3	Control	22	045	24.4
4	Control	28	010	36.9
5	Control	26	354	30.8
6	Control	23	100	22.9
7	Control	30	332	20.4
8	Control	32	338	24.9
9	Small	8	072	32.8
10	Small	32	355	59.6
11	Small	15	000	22.8
12	Small	10	080	51.4
13	Small	29	000	28.2
14	Small	24	030	27.0
15	Small	8	090	31.0
16	Large	28	330	42.1
17	Large	23	030	24.5
18	Large	31	350	31.9
19	Large	25	338	23.5
20	Large	34	030	30.0
21	Large	34	060	36.4
22	Large	25	020	24.6

9.4. APPENDIX D: FORBES ET AL. 2016 FOR. ECOL. MANAGE.

Forbes, A. S., Norton, D. A. and Carswell, F. E. (2015) Tree fern competition reduces indigenous forest tree seedling growth within exotic *Pinus radiata* plantations
Volume 359, 1 January 2016, Pages 1–10
Forest Ecology and Management. doi:10.1016/j.foreco.2015.09.036

9.5. APPENDIX E: TREE FERN COMPOSITION

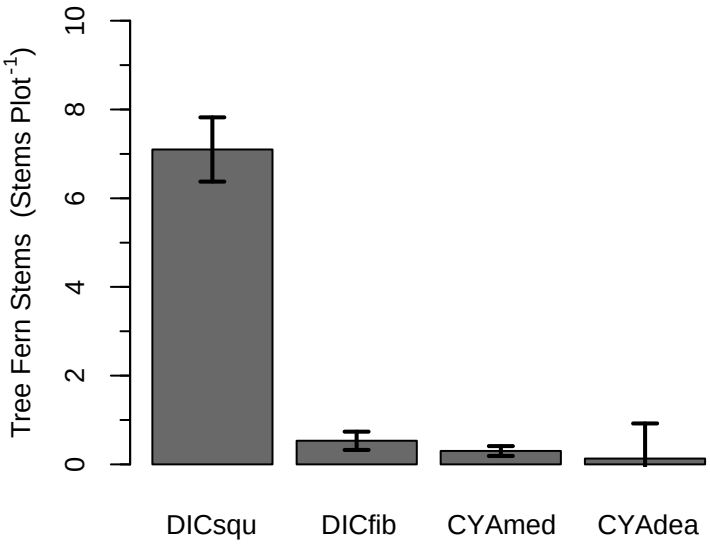

Figure 21. Tree fern composition across 30 experimental plots, within five exotic *P. radiata* plantations aged 36–92-years, located in Kaingaroa Forest, central North Island, New Zealand. Experimental plots represent differing degrees of shade cast by tree fern stands. Columns represent the mean number of tree fern stems per plot for each of the four species. Tree fern plots were surveyed using basal area prism sweep (Factor 4). The data presented is selected from the experimental treatments: tree fern cover intact ("TF"), and tree fern cover removed, prior to removal ("TFR_{before}"). Species codes are: DICsqu = *Dicksonia squarrosa* (*n* = 231), DICfib = *Dicksonia fibrosa* (*n* = 16), CYAmed = *Cyathea medullaris* (*n* = 9), CYAdea = *Cyathea dealbata* (*n* = 4). One specimen of *Cyathea smithii* (*n* = 1) was sampled but is not plotted due to the small sample size. Error bars represent ±1SE.

9.6. APPENDIX F: FORBES ET AL. 2015 ECOL. MANAGE. AND RESTOR.

Forbes, A. S., Norton, D. A. and Carswell, F. E. (2015), Underplanting degraded exotic *Pinus* with indigenous conifers assists forest restoration. Ecological Management & Restoration, 16: 41–49. doi: 10.1111/emr.12137

9.7. APPENDIX G: UNDERPLANTING SITE HISTORY

9.7.1. Vegetation History

Prior to human settlement, *ca*. 730 years ago (Wilmshurst et al., 2008), the Kaingaroa Plateau supported indigenous podocarp-broadleaved forest (Williams & Walton, 2003; Leathwick, 2001, 2004). Vulcanism and associated wildfires (Perry et al., 2014; Vucetich et al., 1960) together with the impacts of human settlement (Boyd, 1992) severely reduced the extent of this forest cover. Consequently, the predominant vegetation at the time of plantation establishment (1920s) was Manuka (*Leptospermum scoparium*) shrubland. Since planting, intensive silvicultural production has prevented the reestablishment of indigenous forest. At the time of underplanting (1962), there was a light understorey cover of small tree ferns and ground ferns, and dead Manuka stems remained from the pre-plantation vegetation at the site (Pardy, 1987).

9.7.2. Podocarp Underplanting Trial

The underplanting trial was established in 1962 within a Ponderosa Pine stand that was established in 1926. Ponderosa Pine seedlings were planted at 1.8 × 1.8 m spacing and left untended. Prior to establishment of the trial, the plantation was affected by a *Dothistroma pini* (fungal pathogen) outbreak which degraded the plantation by thinning the canopy which declined from 20–30% cover in 1975, to 10% cover in 1987, and to the <5% cover today (2013).

In 1958, seeds of Totara, Kahikatea, and Rimu were sourced from central North Island natural forest sites at Minginui and Pureora (C. Low, personal communication, May 20, 2013). Seedlings were raised to four years of age in the New Zealand Forest Research Institute Nursery, Rotorua, and in 1962 a total of 8,900 Totara, 8,900 Kahikatea, and 6,250 Rimu were planted at the underplanting trial site (Pardy, 1987).

Seedlings were planted in north–south orientated lines at uniform 3.6 × 1.8 m spacing (Pardy, 1987). Species were planted in separate stands, being (from east–west) Totara, Rimu, and Kahikatea. As seedlings of all podocarp species were planted at equal spacing, contemporary podocarp stand density is considered a proxy measure of survivorship in this survey. Open-rooted and seedlings with roots encased in moss were planted in alternate rows.

However, no significant differences were found in contemporary growth parameters between those treatments and root treatments were not considered further in this survey. At the time of planting, Kahikatea (0.58 ± 0.017 m) seedlings were significantly taller ($t(4) = 6.34$, $p = 0.004$) than Rimu seedlings (0.44 ± 0.015 m). Totara seedling heights at the time of planting are unknown.

Permanent plots were established at the time of podocarp planting. One *ca*. 14 × 60 m plot were established within each podocarp stand. Kahikatea and Rimu shared one *ca*. 40 × 20 m deer exclosure plot. Rows within plots were marked at both ends and numbered. Individual trees were not permanently labelled and treatment plots were not replicated within podocarp stands. Therefore, permanent plots were not measured directly in this survey as individual tree mortality could not be assessed and additional replication within podocarp stands was required.

9.8. APPENDIX H: CARBON STORAGE CALCULATIONS

Above and below ground carbon stocks were calculated after Beets et al. (2012). The volume (m^3 $tree^{-1}$) of stem and large branches ≥ 10 cm diameter was calculated based on diameter and total tree height data using the allometric formula:

$$V_{stem+br\geq 10} = 4.83 \times 10^{-5} \times (DBH^2 H)^{0.978} \qquad \textit{Equation 1}$$

where DBH is diameter (cm) and H is total tree height (m).

That estimated volume was multiplied by the species-specific wood density (assuming 50% of the mass is carbon) to which mass of branches < 10 cm diameter (over bark) and foliage was added, which gave above ground biomass carbon per tree (kg $tree^{-1}$):

Equation 2

$$C_{agtree} = 0.5 \times d_{stem} \times V_{stem+br\geq 10} + 1.75 \times 10^{-2} \times DBH^{2.20} + 1.71 \times 10^{-2} \times DBH^{1.75}$$

where the constant d_{stem} is a species-specific basic wood density (kg m^{-3}). Basic wood density values used were after Beets et al. (2012): Totara = 370 kg m^{-3}, Kahikatea = 351 kg m^{-3}, and Rimu = 433 kg m^{-3}. The basic wood density used for Ponderosa Pine was 400 kg m^{-3} (SCION unpublished data). Following Beets et al. (2012) we applied the default (Intergovernmental Panel on Climate Change [IPCC], 2003) root/shoot ratio of 25% of the total above ground biomass to accommodate the dry mass of roots, which provided total tree biomass. Carbon storage was then calculated using our stand density (density ha^{-1}) data and expressed as C-stock (t ha^{-1}). Mean C-stock estimates were scaled according to years since planting (podocarps = 51 years, pine = 87 years) to yield a C-stock per annum rate for each species.

9.9. APPENDIX I: UNDERSTOREY FREQUENCY AND COVER

Table 11. Percentage frequency and mean percentage cover of understorey species present within stands of three podocarp species underplanted in a Ponderosa Pine plantation in New Zealand's central North Island

Species	Code	Totara		Kahikatea		Rimu	
		% Freq	Cov	% Freq	Cov	% Freq	Cov
Adiantum cunninghamii	ADIcun	25	0.1				
Asplenium flaccidum	ASPfla	25	0.1	25	0.1	50	0.3
Asplenium oblongifolium	ASPobl	25	0.1				
Asplenium polyodon	ASPpol	25	0.3	25	0.1	100	0.6
Austroderia fulvida	AUSful			25	0.1		
Blechnum discolor	BLEdis					25	0.3
Blechnum fluviatile	BLEflu			50	0.3	75	0.4
Blechnum novae-zelandiae	BLEnov	100	8.6	100	176	100	70.8
Clematis paniculata	CLEpan	25	0.1	50	0.3	75	0.5
Coprosma propinqua	COPpro	50	0.4	50	2.0	75	0.6
Coprosma robusta	COProb	50	0.8	100	6.4	25	0.3
Cyathea smithii	CYAsmi	25	0.3			25	0.9
Dacrydium cupressinum	DACcup					25	0.6
Dacrycarpus dacrydioides	DACdac			75	0.9	25	0.1
Dicksonia fibrosa	DICfib	25	0.8	100	15.5	75	6.8
Dicksonia squarrosa	DICsqu	100	125.4	50	3.1	75	3.3
Gaultheria antipoda	GAUant					25	0.1
Histiopteris incisa	HISinc			25	0.1		
Leucopogon fasciculatus	LEUfas			25	0.1	75	0.8
Microsorum pustulatum	MICpus					25	0.1

Species	Code	Totara		Kahikatea		Rimu	
		% Freq	Cov	% Freq	Cov	% Freq	Cov
Orchidaceae sp.	–	75	0.4			75	0.4
*Osmunda regalis**	OSMreg			25	0.1		
Paesia scaberula	PAEsca			25	0.1	25	0.1
Parsonsia capsularis	PARcap			100	0.8	50	0.3
Polystichum vestitum	POLves			75	1.5	50	0.3
*Pseudotsuga menziesii**	PSEmen	75	0.4	25	0.1	50	0.3
Pteridium esculentum	PTEesc					25	0.1
*Rubus fruticosus**	RUBfru	75	0.5	100	1.8	75	0.5
Rumohra adiantiformis	RUMadi					50	0.3
Uncinia sp.	–					50	0.3

Note. % Freq = percentage frequency; Cov = mean percentage cover; * = exotic species.

9.10. APPENDIX J: SIMILARITY PERCENTAGE ANALYSIS

Table 12. Dissimilarly values among podocarp stands (SIMPER analysis) based on weighted cover-abundance (WCA) of understorey species. Standard deviation in parenthesis. Species codes are listed in Appendix I

Totara and Kahikatea Species	Mean WCA Totara	Mean WCA Kahikatea	Contribution (%)	Cumulative (%)
DICsqu	13.25	2.00	20.05(± 6.3)	30.82
BLEnov	4.50	12.00	13.48(± 4.6)	51.53
DICfib	0.75	4.50	6.78(± 3.3)	61.95
COProb	1.50	3.88	4.88(± 3.3)	69.44
Totara and Rimu Species	**Mean WCA Totara**	**Mean WCA Rimu**	**Contribution (%)**	**Cumulative (%)**
DICsqu	13.25	1.25	24.85(± 7.4)	38.05
BLEnov	4.50	7.63	7.34(± 4.6)	49.29
DICfib	0.75	3.50	6.25(± 4.2)	58.87
LEUfas	0.00	1.50	0.03(± 1.8)	63.34
COProb	1.50	0.50	0.03(± 0.02)	67.60
Kahikatea and Rimu Species	**Mean WCA Kahikatea**	**Mean WCA Rimu**	**Contribution (%)**	**Cumulative (%)**
BLEnov	12.00	7.63	7.95(± 4.7)	16.21
COProb	3.88	0.50	5.72(± 4.0)	27.88
DICfib	4.50	3.50	3.81(± 3.8)	35.65
DICsqu	2.00	1.25	3.60(± 3.4)	42.99
COPpro	1.75	1.25	3.20(± 2.5)	49.53
POLves	2.00	0.50	2.85(± 1.7)	55.35
RUBfru	2.38	0.88	2.81(± 1.9)	61.90
LEUfas	0.25	1.50	2.42(± 1.6)	66.03
CYAsmi	0.00	1.00	1.96(± 3.5)	70.04

9.11. APPENDIX K: NORTON & FORBES 2013 APPL. VEG. SCI.

Norton, D. A., Forbes, A. (2013), Can exotic pine trees assist in restoration?. Applied Vegetation Science, 16: 169–170. doi: 10.1111/avsc.12014